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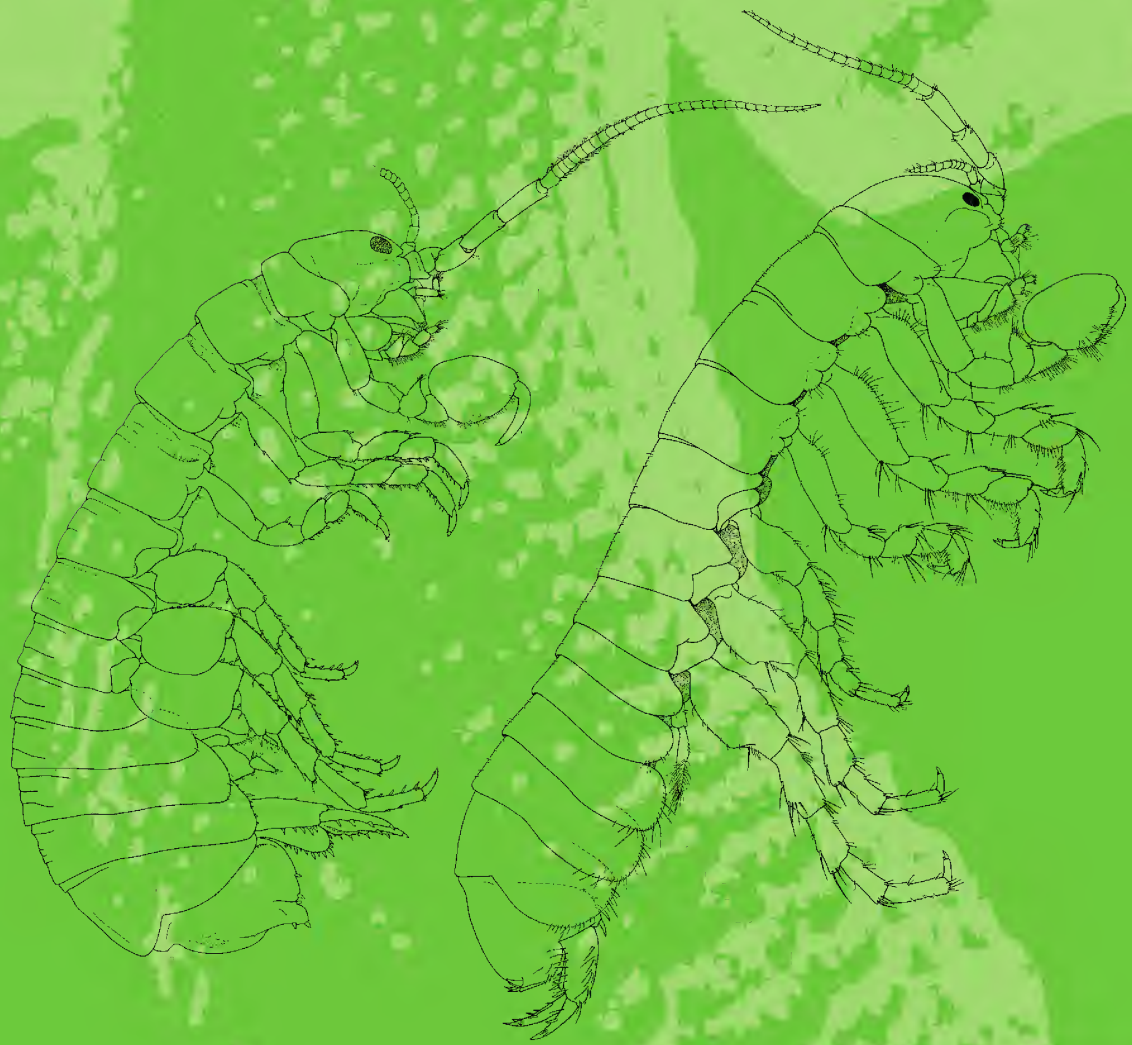

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RECORDS OF THE AUSTRALIAN MUSEUM

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The **cover illustrations**—original pencil drawings by Australian Museum scientist Dr Stephen Keable—are of two new species within two new genera of Western Australian phreatoicid isopods: *Eremisopus beei* (left) and *Platypyga subpetrae* (right). The existence of considerable undescribed diversity is foreshadowed by these discoveries in the crustacean suborder Phreatoicidea (Wilson & Keable, 2002, *Records of the Australian Museum* 55[1]). The faded impression (original photo by G.C. Clutton) of a Solomon Islands skink lizard—*Tribolonotus ponceleti* Kinghorn, 1937—which was also first described in an earlier issue of *Records of the Australian Museum* 20(1), provides background.

Since 1999 Australian Museum Scientific Publications have been released as PDF files, at our website, free of charge and six months after publication. The above description of the new species *E. beei* and *P. subpetrae* can be viewed at www.amonline.net.au/pdf/publications/1359_complete.pdf or purchased as part of a bound issue (AU$50.00) from the Australian Museum Shop.

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Taxonomy, Phylogeny and Zoogeography of the Subfamily Ceratomerinae of Australia (Diptera: Empidoidea)

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ABSTRACT. Nineteen endemic Australian species of the Gondwanan genus *Ceratomerus* Philippi are revised, including four described and 15 new species: *C. albistylus* Hardy, *C. athertonius* n.sp., *C. attenuatus* n.sp., *C. barringtonensis* n.sp., *C. bickeli* n.sp., *C. bulbosus* n.sp., *C. campbelli* (Paramonov), *C. falcatus* n.sp., *C. globosus* n.sp., *C. hibernatus* n.sp., *C. inflexus* Hardy, *C. lobatus* n.sp., *C. maculatus* n.sp., *C. malleolus* n.sp., *C. macalpinei* n.sp., *C. ordinatus* Hardy, *C. oreas* n.sp., *C. orientalis* n.sp., and *C. victoriae* n.sp. This is primarily an aquatic genus, restricted to cascading rocky rainforest streams of eastern Australia from the Tablelands near Cairns to Tasmania. Adults prey on flying aquatic insects and are collected on emergent rocks and riparian vegetation.

The Australian ceratomerine fauna comprises three species groups, with the *C. campbelli* group apparently most closely related to the *C. paradoxus* group of Chile. The *C. ordinatus* group appears closely related to species from New Zealand and Ecuador (high elevations). A key to all Australian species is included and zoogeography discussed.

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The aquatic Diptera of Australia are relatively poorly known, with the exception of economically important groups such as Tabanidae, Simuliidae and Culicidae. In the Empidoidea, two subfamilies dominate cascading streams in eastern Australia. Firstly, the Clinocerinae, include at least three genera (*Proagomyia* Collin, *Asymphyloptera* Collin and *Clinocera* Meigen). *Clinocera* includes seven species (Sinclair, 2000b), while there are some 6–8 spp. of *Asymphyloptera* and possibly as many *Proagomyia* (Sinclair, unpubl. data).

The second subfamily is the Ceratomerinae, which is particularly common on emergent rocks in mountainous streams of eastern Australia. Besides these taxa, other empidoids collected on emergent rocks include *Hilara* Meigen (but more often swarming and skimming pools), *Apalocnemis* Philippi, *Hydropeza* Sinclair (1999), and several undescribed genera (e.g., "Genus No.3" Sinclair & Cumming, 2000). A number of dolichopodid species are also known to frequent river rocks as discussed by Bickel (1994). However, it is the Ceratomerinae that most often dominate this niche in Australia.

The Ceratomerinae are confined to wet forests of the former Gondwanan continents of Australia, New Zealand and South America. Despite its classic Trans-Antarctic distribution, these flies have received sparse attention from zoogeographers, because of the lack of knowledge at both the species and genus level and absence of published data on phylogenetic relationships within this subfamily.

Adults of Ceratomerinae are characterized by long, narrow wings and very elongate antennae, which strongly project forward as they run about. In Australia, the Ceratomerinae are represented by the single genus *Ceratomerus* Philippi, 1865,

first described from Chile. There are four described and 15 new Australian species described in this paper. In New Zealand, there are 13 named species (Plant, 1991), but more than twice this number remain undescribed (Sinclair, 1998).

Very little is known about the biology of this subfamily, the immature stages remain unknown but are presumed to be primarily aquatic. This is the second of a series of studies on the subfamily Ceratomerinae (see Sinclair, 1997), with the present study confined to the taxa of Australia.

Materials and methods

This study is based on some 1850 adult specimens of *Ceratomerus* borrowed from or deposited in the following institutions: Australian Museum, Sydney, Australia (AMS); Australian National Insect Collection, Canberra, Australia (ANIC); The Natural History Museum, London, England (BMNH); Bernice P. Bishop Museum, Honolulu, USA (BPBM); Canadian National Collection of Insects, Ottawa, Canada (CNC); Museum of Victoria, Melbourne, Australia (MVM); University of Queensland Insect Collection, Brisbane, Australia (UQIC); United States National Museum of Natural History, Washington, USA (USNM); N.E. Woodley Collection [private], Washington, USA (WOOC); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK). Abbreviations given here are used throughout the text to indicate deposition of specimens.

Although the Hardy collection was donated to the Australian Museum (Chadwick, 1966), his type specimens of *Ceratomerus* could not be located. According to Daniels (1978) many types from this collection were found to be damaged or destroyed when it was received at AMS. The three species of *Ceratomerus* described by Hardy were not included in Daniels' (1978) list. A search of the ANIC, UQIC and Queensland Museum (Brisbane) proved unsuccessful, and consequently the types are presumed destroyed and lost.

Terms used for adult structures primarily follow those of J.F. McAlpine (1981), except male terminalia where terms of Cumming *et al.* (1995) and Sinclair (2000a), and antenna where terms of Stuckenberg (1999) are used. The apical portion of male abdomens were macerated in hot 85% lactic acid in order to examine and draw the terminalia. The following abbreviations were used in the descriptions: ad, anterodorsal; av, anteroventral; dc, dorsocentral bristle; npl, notopleural bristle; pal, postalar bristle; pd, posterodorsal; pprn, postpronotal bristle; presut spal, presutural supra-alar bristle; psut spal, postsutural supra-alar bristle; pv, posteroventral; S, sternite; sctl, scutellar bristle; T, tergite. The following additional abbreviations were used in recording the label data: BJS, B.J. Sinclair; ck, creek; DHC, D.H. Colless; DJB, D.J. Bickel; DKM, D.K. McAlpine; FlR, Flora Reserve; FR, Forest Reserve; MT, malaise trap; NP, National Park; nr, near; SF, State Forest; SP, State Park; str., stream; y.pans, yellow pan traps.

The term "bristle" is used for differentiated large setae on the head, mesonotum and legs bearing a particular name or one of a series with a particular name, e.g., notopleural bristle, dorsocentral bristle, anterodorsal bristle. Label data of holotypes are cited in full, with original spelling, punctuation and date. Lines are delimited by a slash mark(/), a semicolon separates data quoted from different labels, and author's remarks are given in square brackets.

A variety of sampling methods proved effective in collecting Ceratomerinae, especially when used in combination. The traditional methods of sweeping and aspirating adults directly off emergent rocks lying in cool, cascading streams proved very successful. Wading up streams and watching the flies dart about on the rocks assisted in locating specimens. This proved especially effective for species of the *C. campbelli* group, which were observed to fly close to the water surface and dart beneath emergent rock. From here the specimens were aspirated.

Shallow, yellow, plastic pan traps, filled with water and a few drops of detergent to break the surface tension were also highly effective in attracting and capturing specimens of Ceratomerinae. These methods are also very productive for other Empidoidea (see Pollet & Grootaert, 1987; Bickel, 1994; Sinclair & Cumming, 2000). The yellow pans (simply small cereal bowls) were spread beside and along streams and rivers, or placed on emergent rocks, especially at small cascades. Many of the large series and some rare Tasmanian species were collected using yellow pans. Pans were left out for a maximum of 24 hours then collected and redistributed at other localities.

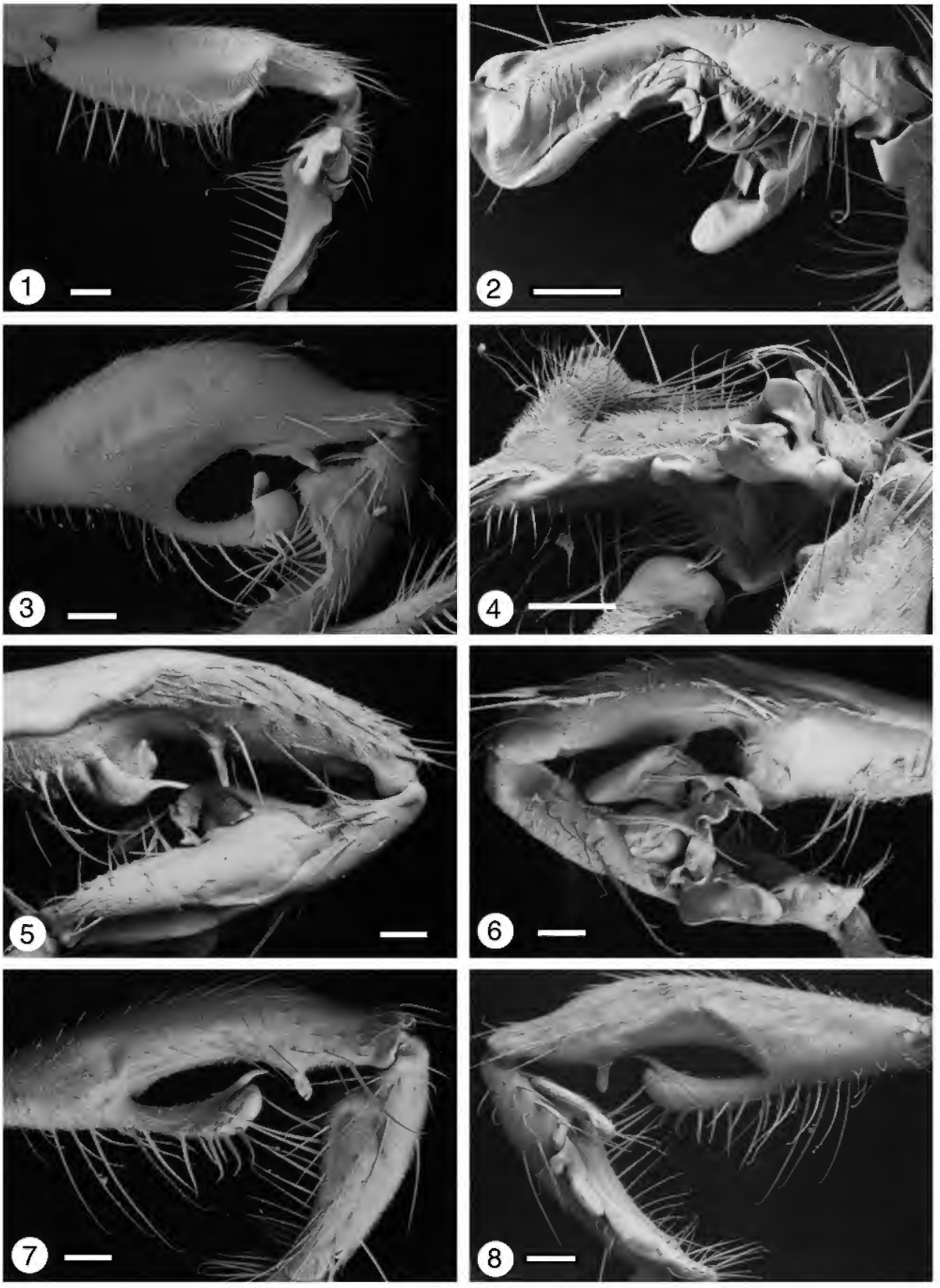
Morphology

Antenna. The most characteristic defining feature of the Ceratomerinae is the presence of a conus or thumb-like condyle arising from the apex of the pedicel (or second antennal segment), which is inserted into the postpedicel (or first flagellomere) (Figs. 58–60). In the majority of Empidoidea, the conus is absent and the base of the postpedicel is narrowed and inserted into an apical invagination of the pedicel. The conus is inserted on the median side (laterally) of the postpedicel in all Ceratomerinae. A similar condition also occurs in some genera of the Sympycninae (Dolichopodidae), including *Syntormon* Loew and *Parasyntormon* Wheeler (Bickel, 1999 and pers. comm.). In Dolichopodinae, a similar conus is present, but it is inserted medially into the postpedicel. This latter form of conus also occurs in Cyclorrhapha, except Platypezidae and Opetiidae (Cumming *et al.*, 1995). On the basis of many conflicting characters and the differences in insertion, it is assumed that the presence of the conus is derived independently among all the above groups.

Wing venation. The Ceratomerinae, exclusive of *Glyphidopeza* Sinclair are also characterized by distinct wing venation. The wing is greatly narrowed with the anal lobe not developed, R_1 terminating in the costa prior to the mid-length of the wing, and the cell cu*p* (or anal cell) is absent (Figs. 10, 16, 51, 87). The dm cell is usually narrow, rectangular and parallel-sided (except where secondarily modified in some males), emitting two veins (M_{1+2} and CuA_1). The basal cells lack a clear separating vein, with cell bm only weakly outlined by a faint line and some colour differentiation within the cell.

Male secondary sexual characters. Many species of Ceratomerinae have species-specific male secondary sexual characters. These include modifications of the antenna, labrum and labium, modifications of wing veins, posterior margin of the wing, fore and/or midlegs, occasionally hindlegs, and pleura region of some New Zealand species. The male midleg can be grotesquely modified as seen in the *C. campbelli* group (Figs. 1–8). These modifications are presumably used in courtship and evolved through sexual selection by female choice.

Male terminalia. The male terminalia of Ceratomerinae, particularly *Ceratomerus*, have not been adequately



Figs. 1–8. Scanning electron micrographs of male midlegs of *Ceratomerus*. 1–2, *C. athertonius*: 1, midleg, anterior view; 2, mid tibia, dorsal view. 3–4, *C. barringtonensis*: 3, midleg, posterior view; 4, tibia, anterior view. 5–6, *C. campbelli*: 5, posterior view; 6, anterior view. 7–8, *C. victoriae*: 7, posterior view; 8, anterior view. Scale bars = 0.1 mm.

described. Collin (1933) provided an excellent illustration of *C. mediocris* Collin, but the components were unlabelled. The illustration of the same species in Chvála (1983, figs. 128–131) has several inaccuracies, which lead to misinterpretations of homologies. The homologies of the male terminalia proposed by Chvála (1983) are rejected here in favour of those of Cumming *et al.* (1995). In addition, this Chilean species is particularly complex and not an appropriate example of this genus.

Generally the terminalia are somewhat arched dorsally over the abdomen with tergite 7 weakly sclerotized medially and tergite 8 greatly narrowed dorsally. The hypandrium is cup-shaped and elongate, often with the posterior margin projecting as a long, thin extension (Figs. 23, 103, 111, 115). This projection may function as some sort of phallic brace. A pair of distinct gonocoxal apodemes project anteriorly from the anterodorsal margin of the hypandrium. Postgonites are paired processes located near the phallus and are homologous to similar structures in the Cyclorrhapha (Sinclair, 2000a). They appear as arched, articulated processes arising at the base of the phallus, just above the ejaculatory apodeme. They are usually sickle-shaped (Fig. 115), or nearly straight (Fig. 121) and occasionally divided into two pairs (Fig. 77).

The two epandrial lamellae are not connected dorsally (Fig. 113) as observed in the ground plan of the Empidoidea. The lamellae are held rigid by narrow anteroventral extensions to the hypandrium and internally by the bacilliform sclerites and subepandrial plate. The epandrial lamellae are sometimes greatly inflated in some Australian species, particularly of the *C. inflexus* group (Fig. 45). Epandrial lobes are sometimes developed (Figs. 30, 120) often closely associated with the surstylus. Large lateral spine-like setae are also present in some species (e.g., *C. barringtonensis* n.sp., Fig. 19).

The phallus is a narrow, tapered tube projecting from the posterior half of the hypandrium. In some species the phallus appears as a pair of apical processes or as sickle-shaped processes (Fig. 121). The base of the phallus extends anteriorly to the subepandrial sclerite + hypandrium point of junction (point y). The ejaculatory apodeme is a large vertically orientated plate, fused to the base of the phallus (Fig. 114). This configuration also occurs in the Trichopezinae and Brachystomatinae.

The cercus is normally well sclerotized posteriorly and it is this face that extends ventrally to articulate with the subepandrial sclerite or bacilliform sclerite. The anterior face of the cercus is mostly membranous, lightly pigmented with numerous setae especially long and stout surrounding the anus (Figs. 17, 19, 110, 113, 120). The form of the cercus can be species-specific and uniquely modified in some species (e.g., *C. macalpinei* n.sp. [Fig. 69] and *C. oreas* n.sp. [Fig. 72]).

The subepandrial sclerite is a narrow transverse plate with lateral extensions posteriorly or what are termed bacilliform sclerites, which form the inner walls of the surstylus apically. The surstyli are highly variable, ranging from poorly differentiated lobes in some species (e.g., *C. maculatus* n.sp., Fig. 102), to long, slender, unarticulated lobes (e.g., *C. campbelli* (Paramonov), Fig. 22), or strongly articulated lobes (e.g., *C. albistylus* Hardy, Fig. 110).

The most noticeable difference between the Australian and New Zealand *Ceratomerus* fauna is the great morphological variability of the male terminalia in the former. The Australian species are easily identified on the basis of genitalia alone, while identification among New Zealand species is more reliant on external features, such as male secondary sexual characters. It is likely that male secondary sexual characters are used during complex courtship behaviour in many New Zealand species. Several Australian species are clearly closely related on the basis of the configuration of the male genitalia. For example, (*C. inflexus* n.sp., *C. bulbosus* n.sp., *C. bickeli* n.sp.) and (*C. malleolus* n.sp., *C. macalpinei* n.sp.).

Ceratomerinae

Ceratomerinae Collin, 1928: 3. Type genus *Ceratomerus* Philippi, 1865.

This subfamily includes the following genera: *Ceratomerus* Philippi, *Glyphidopeza* Sinclair, and *Icasma* Collin.

Diagnosis. Dichoptic in both sexes, usually lacking ommatrichia. Long projecting antennae generally inserted high on head; first antennal segment (scape) more than twice as long as the second segment (pedicel), bearing long dorsal and ventral setae; pedicel with finger-like condyle or conus on which postpedicel is inserted laterally; postpedicel (first flagellomere) elongate, often strap-like. Proboscis long and projected, longer than length of head; pseudotracheae lacking, except *Glyphidopeza*; lacinia freely projected, except fused to labium in *Glyphidopeza*.

Scutum with restricted rows of bristles, sometimes reduced in number and size. Dorsal mesepimeral pocket present; laterotergite bare.

Wing narrow, lacking anal lobe; Sc complete, or incomplete in *Icasma*; R_{4+5} branched or unbranched; cell cu*p* absent, except *Glyphidopeza*; 2 veins usually emitted from cell dm, or M_{1+2} petiolate, except *Glyphidopeza* with 3 veins.

Male terminalia arched dorsally; ejaculatory apodeme plate-like, narrowly fused to base of phallus; epandrial lamellae not connected anterodorsally; surstyli usually weakly articulated with epandrium. Female terminalia truncate withdrawn into segment 7; sclerites of segment 8 articulated anterolaterally; anterior margin of tergite 8 with median or pair of flattened plates or none; tergite 10 (acanthophorites) arched dorsally, bearing spines or stout setae; cercus heavily sclerotized, projecting dorsally; spermatheca with single spherical receptacle.

Historical review of the classification of the Ceratomerinae

The genus *Ceratomerus* was described by Philippi (1865) for a highly modified male species from Chile which has a large protuberance or horn on the mid femur. Melander (1928) tentatively included *Ceratomerus* in the subfamily Clinocerinae because its slender legs and shortened front coxa are similar to that of the latter. In his revision of New Zealand Empididae, Collin (1928) erected a new subfamily Ceratomerinae for this genus, and has been followed ever since. In this revision, four new species of *Ceratomerus* and a new monotypic genus *Icasma* were described. Collin (1933) later described two species of *Ceratomerus* from southern Chile. In Australia, Hardy (1930) and Paramonov (1961) described four and one new species, respectively. No additional species of this subfamily were described until Plant (1990, 1991) described one and seven new species of *Icasma* and *Ceratomerus*, respectively.

Most recently, Sinclair (1997) described five new species of *Icasma* and two new species of a new genus *Glyphidopeza*, all endemic to New Zealand. In an ongoing revision of this subfamily, many new species remain to be described from New Zealand and there are at least two undescribed genera from South America (Sinclair, 1998).

Chvála (1983) assigned the subfamily as the sister group to the Clinocerinae, but provided little evidence for such an arrangement, except for general resemblance of the male terminalia with that of the Clinocerinae. Ceratomerinae was considered the sister group to Hemerodromiinae + (Brachystomatinae + Clinocerinae) by Wiegmann *et al.* (1993), but these relationships are weakly supported as discussed by Sinclair (1995: 671, 719). Presently, the Ceratomerinae is considered most closely related to the Trichopezinae and Brachystomatinae because of unique similarities of the female terminalia and form of the male ejaculatory apodeme (Sinclair, 1995; Cumming *et al.*, 1995; Cumming & Sinclair, 2000). These three subfamilies comprise a probable new family group within the Empidoidea (Cumming & Sinclair, 2000).

In contrast to its phylogenetic position within the Empidoidea, the monophyly of the Ceratomerinae has never been questioned. A number of characters are derived in comparison to the Trichopezinae and Brachystomatinae including: a small conus projecting from the second antennal segment into the postpedicel, scape 2–3 times longer than pedicel, inner face of base of scape flattened, males dichoptic, R_1 terminates proximally to mid-length of wing, and dorsal bridge of epandrial lamellae lacking.

Bionomics

The Ceratomerinae of Australia are confined to the area immediately within and along rocky, cascading streams of the eastern ranges. These streams are surrounded by a range of rainforest vegetation types that have been classified into numerous floral systems, comprehensively appraised by Adam (1992). Rainforest is discontinuously distributed in eastern Australia, and represent remnants of a widespread wet vegetation that predominated in the Late Paleocene and Early Eocene (White, 1994; Bickel, 1994). Since this time, the progressive drying phases which accelerated during the Miocene have fragmented the rainforest into disjunct refugia. However, many of these pockets of rainforest are not completely isolated, but are connected through "gallery" or gully forests—a mixture of sclerophyll-rainforest vegetation along streams (Adam, 1992; Bickel, 1994). These strips of rainforest along watercourses may extend well beyond lower rainfall regions and provide continuity and pathways among major stands. This is especially true around Sydney, which is surrounded by dry sclerophyll and heathlands, with narrow strips or patches of rainforests with closed overhead canopies growing along streams flowing through narrow valleys. It is in these habitats that a number of fairly widespread species of Ceratomerinae were collected, especially in the coastal lowlands around Sydney (e.g., Bola, Couranga and Waterfall Creeks).

The Australian species of Ceratomerinae are both steno- and eurythermic, some being found in a variety of stream temperatures. For example, *C. victoriae* n.sp. is known only from heavily shaded, cool streams cascading through temperate rainforests usually dominated by *Nothofagus*. In Victoria, these habitats are now confined to small patches, predominantly in deep ravines and consequently the populations of *C. victoriae* n.sp. are rather isolated (Fig. 28). In contrast, *C. orientalis* n.sp. is tolerant of a wide range of stream temperatures. This tolerance has facilitated its widespread distribution, and it is the most commonly collected species of Ceratomerinae in Australia.

Most Australian species are found primarily in streams, running about on emergent rocks (especially *C. ordinatus* group) with their antennae outstretched. Only one species, *C. albistylus* is most commonly collected more distantly from streams. A large number of specimens of *C. victoriae* n.sp. were collected by sweeping fronds of tree ferns that were overhanging streams.

Although several distinct larval empidoid types have been identified from stream and river surveys, the larval and pupal stages of Ceratomerinae remain unknown. In addition, the mating habits have not been observed. Attempts were made to identify the immature stages by collecting live females and inducing oviposition by decapitation (see Cumming & Cooper, 1993), but these attempts failed. Since adults of most species of Australian *Ceratomerus* are present nearly year round, prediction of the emergence period(s) is difficult. In collections examined, some female specimens collected in October and November appeared to have swollen abdomens indicating a gravid condition. This is possibly the most appropriate period for attempts at either collection of immature stages of this subfamily or decapitation of gravid females.

Adults are believed to be predacious (except probably the *C. virgatus* group from New Zealand). Adults of *C. ordinatus* Hardy were observed feeding on conspecific flies that were squashed on emergent rocks. Numerous adults of this species were observed running about on emergent rocks in the Franklin River (Tasmania). They easily and quickly found the squashed corpses and extended their long proboscises obliquely while feeding. The morphology of the labrum (i.e., presence of apical epipharyngeal blades) supports predacious habits. Chvála (1983: 78) hypothesized that adults of Ceratomerinae were flower visitors on the basis of their long *Empis*-like proboscis, but only specimens of the *C. virgatus* group from New Zealand have been collected on flowers.

Ceratomerus Philippi

Ceratomerus Philippi, 1865: 765. Type-species *Ceratomerus paradoxus* Philippi (monotypy).

Tomia Paramonov, 1961: 100 nec Martynov (1936: 1262). Type-species *Tomia campbelli* Paramonov (original designation) (Colless & D.K. McAlpine, 1991: 760).

Notes on synonymy. *Tomia* Paramonov was erected for the highly autapomorphic species *C. campbelli*, but the extreme morphological features are not unusual for the genus *Ceratomerus*, and Colless & D.K. McAlpine (1991) were justified in this synonymy. In addition, *Tomia* Paramonov is a junior homonym of *Tomia* Martynov (1936), a fossil Paraplecopteran of the family Tomiidae (Rohdendorf, 1991).

Diagnosis. This genus is distinguished from other Ceratomerinae by the following combination of characters: posterior ocelli usually widely separated with ocellar bristles inserted anteriorly, postpedicel lengthened and tapered apically, acrostichal setulae present, 3–5 dorsocentral bristles present, Sc complete, R_{4+5} branched, cell dm emitting 2 veins (M_{1+2} and CuA_1), cell cup absent, presence of

distinct bristles on tibiae, scutum not highly polished, and abdominal sclerites not heavily sclerotized and punctate.

Description. Male. *Head*. Dichoptic, bare; face parallel-sided; frons slightly narrowed above antennae; posterior ocelli usually widely separated with ocellar bristles inserted anteriorly. Antenna with scape at least 2 times length of pedicel; pedicel normally ovate, sometimes slightly to greatly lengthened; postpedicel with quadrate base, attenuated and strongly prolonged apically; occasionally apical segments (8–10) fused to postpedicel. Proboscis long, slender; labrum long, stout, with pair of apical epipharyngeal blades; lacinia free, blade-like; pseudotracheae absent.

Thorax. Antepronotum usually with stout pair of setae; scutum generally completely clothed in fine, pale pruinescence; acrostichal setulae uniserial or biserial, rarely absent; 3–5 dc; 1–2 npl, 1–2 pairs sctl; laterotergite bare.

Wing long and narrow; stigma absent or present at apex of R_1 or apex of cell r_1; Sc complete; C circumambient; R_{4+5} branched; cell dm emitting 2 veins (M_{1+2} and CuA_1); cell cu*p* absent.

Abdomen. Sclerites usually not heavily sclerotized; lacking punctate appearance.

Terminalia. Hypandrium narrow with pair of divergent postgonites, gonocoxal apodemes short and slender, somewhat projected beyond hypandrium. Phallus short with plate-like ejaculatory apodeme fused to base of phallus. Epandrial lamellae separated, lacking dorsal bridge ventral to cercus; surstylus weakly to strongly articulated. Cercus membranous to strongly sclerotized, often with long apical setae and long setae surrounding anus.

Female. *Terminalia*. Posterior margin of T7 with row of setae. T8 articulated anterolaterally with S8; anterior margin with pair of flattened plates, single, rounded median plate, or margin straight (plates absent); posterior margin with median membranous cleft; medially with transverse row of setae. S8 with slender ventral setae, membranous posteriorly. T10 with 1 or more posterior rows of acanthophorite spines of various sizes. Cercus held upright, slightly arched, bearing apically numerous spine-like bristles similar to acanthophorite spines on T10, posterior margin with long, slender setae. Spermathecal receptacle spherical, darkly pigmented on long, unpigmented duct.

Remarks. This genus is recorded from Australia, New Zealand and South America. There are 19, nearly 40, and five species known from Australia, New Zealand and South America, respectively. The above generic concept of *Ceratomerus* is based on the examination of all known species of Ceratomerinae, which is the preliminary result of an on going phylogenetic analysis reported by Sinclair (1998).

Key to males of the Australian species of *Ceratomerus**

Ceratomerus can be distinguished from all other Australian empidoids by the following features: cell cu*p* absent, first flagellomere very large with pedicel inserted thumb-like on inner side at base, proboscis long and slender, arising from front of mouth-opening and slightly recurved. Although males are unknown for *C. hibernatus*, it is included in the key based on characters that are independent of the sex of the specimen.

1 Stigma absent (Figs. 80–84); second antennal segment (pedicel) long, at least one-fourth length of first segment (Figs. 59, 60); acrostichal setae directed posteriorly (*C. ordinatus* group) 2

—— Stigma present (Figs. 9, 16, 87); second antennal segment (pedicel) short, globular, less than one-fourth length of first segment (Figs. 25, 58); acrostichal setae usually directed anteriorly 5

2 Auxiliary crossvein present between R_{2+3} and R_4 (Figs. 80, 83) or wing highly modified (Fig. 82); median fork usually distal to radial fork 3

—— Auxiliary crossvein absent, wing unmodified (Figs. 81, 84); median fork proximal to radial fork 4

3 Veins on wing wavy, highly modified, membrane with dark patches; cell dm distally emitting 3 veins (Fig. 82) ..... *C. maculatus* n.sp.

—— Veins on wing straight, not modified; cell dm distally emitting 2 veins, median vein petiolate (Fig. 80) ..... *C. falcatus* n.sp.

(An undescribed specimen from Philip Is. [Norfolk group] may also key to this species).

4 Median fork separated from radial fork by less than length of crossvein dm-cu (Fig. 84); apical third of hind tibia with row of 4–5 anterodorsal bristles (Fig. 94) ..... *C. ordinatus* Hardy

—— Median fork separated from radial fork by more than length of crossvein dm-cu (Fig. 81); apical third of hind tibia with 2 anterodorsal bristles ..... *C. hibernatus* n.sp.

* Ceratomerinae can be identified from other empidoids using the key to the major lineages of Australian Empidoidea in Sinclair & Cumming (2000).

5 Male midleg not highly modified, with dense ventrobasal setae on femur only (Figs. 38, 41); tibia cylindrical 6

—— Male midleg highly modified, with lobes, modified setae and strongly attenuated forming pockets (Figs. 1–8, 39, 93, 97) 13

6 R_{2+3} distinctly deflected around stigma (Figs. 53–56); in doubtful cases epandrial lamellae nearly spherical and inflated (*C. inflexus* group) 7

—— R_{2+3} not distinctly deflected around stigma (Figs. 16, 87); epandrial lamellae not inflated 12

7 Epandrial lamellae strongly inflated, nearly spherical, much wider than abdomen (Figs. 44–46); cercus variable 8

—— Epandrial lamellae not highly inflated, simply convex, less than width of middle of abdomen; cercus short, broad, with inner stout setae (Fig. 72) ..... *C. oreas* n.sp.

8 Hypandrium with pair of long, slender, posterior processes, longer than width of epandrium (Fig. 44) ..... *C. bickeli* n.sp

—— Hypandrial processes short, projecting only slightly beyond epandrium (Figs. 46, 63, 66) 9

9 Tergites 4–6 with heavily sclerotized, dark ventrolateral ridges (Fig. 68); cercus anvil-shaped, clothed with dense macrotrichia, lacking stout setae; base of cercus with pair of long processes (Figs. 66, 69) 10

—— Tergites 4–6 lacking ridges; cercus gradually expanded apically with tufts of stout, apical setae; base of cercus lacking long processes (Figs. 46, 63) 11

10 Anepisternum with pale streak across lower half; lobe beneath the cercus roundly expanded apically; posterior tip of cercus tapered (Fig. 69) ..... *C. macalpinei* n.sp.

—— Anepisternum uniformly brown, lacking pale zone on lower half; lobe beneath the cercus tapered, apex setose; posterior tip of cercus round (Fig. 66) ..... *C. malleolus* n.sp.

11 Anterior hypandrial process truncate; posterior hypandrial process broad (Fig. 63) ..... *C. inflexus* Hardy

—— Anterior hypandrial process bilobed; posterior hypandrial process narrow (Fig. 46) ..... *C. bulbosus* n.sp.

12 Apical portion of postpedicel shorter than rectangular basal portion; stylus (segments 8–10) subequal to or longer than postpedicel; cercus very slender and long, with short lateral setulae (Fig. 34) ..... *C. attenuatus* n.sp.

—— Apical portion of postpedicel longer than rectangular basal portion; stylus (segments 8–10) shorter than postpedicel; cercus hooked posteriorly, expanded basally (Fig. 120) ..... *C. orientalis* n.sp.

13 Scutum with 3 dorsocentral bristles, prescutellar bristles short and inconspicuous; male postpedicel greatly lengthened, gradually tapered, stylus greatly shortened (Fig. 61); femora and halter yellow ..... *C. albistylus* Hardy

—— Scutum with 4 dorsocentral bristles, prescutellar bristles short and slender; male postpedicel not lengthened, strongly tapered, stylus longer than one-half length of postpedicel; femora distinctly darker apically; halter dark 14

14 Stigma short, not extending proximally to radial fork (Fig. 86); pleura bright yellow; mid femur with 3 flattened anterior setae on basal third ..... *C. lobatus* n.sp.

—— Stigma extending proximally to radial fork (Fig. 51); in doubtful cases pleura dark; mid femur lacking flattened anterior setae 15

15 Anal lobe of wing produced, bearing long slender processes or long setae (Figs. 9, 12); epandrium not enclosing hypandrium; pleura yellow to pale brown (*C. campbelli* group) 16

—— Anal lobe of wing not produced, lacking processes and long setae (Fig. 51); epandrium completely enclosing hypandrium (Fig. 48); pleura dark brown ..... *C. globosus* n.sp.

16 Anal lobe of male wing with 3 long, slender processes (Figs. 9, 11, 13); costal margin lacking long, dorsal setae; mid femur lacking long ventral lobe 17

—— Anal lobe of male wing with long setae, lacking slender processes (Figs. 12, 14); costal margin with long, dorsal setae; mid femur with long ventral lobe 18

17 Acrostichal setulae absent; pleura with at least laterotergite and meron dark; hind femur lacking long, flattened posteroventral setae ..... *C. athertonius* n.sp.

—— Acrostichal setulae present; pleura usually with only laterotergite dark; hind femur with long, flattened posteroventral setae ..... *C. campbelli* (Paramonov)

18 Pleura yellow with brown smudges; mid femur greatly swollen (Fig. 3); anal lobe of wing truncate, with long, wavy, slender setae (Fig. 12) ..... *C. barringtonensis* n.sp.

—— Pleura yellow, lacking brown smudges; mid femur not greatly swollen (Fig. 7); anal lobe of wing acutely produced, with stout setae (Fig. 14) ..... *C. victoriae* n.sp.

Key to Females of the Australian species of *Ceratomerus*

Females of *Ceratomerus bickeli* are unknown.

1 Stigma absent (Fig. 81); second antennal segment (pedicel) long, at least one-fourth length of first segment (Fig. 89); acrostichal setae directed posteriorly (*C. ordinatus* group) 2

—— Stigma present (Fig. 15); second antennal segment (pedicel) short, globular, less than one-fourth length of first segment (Fig. 62); acrostichal setae usually directed anteriorly 4

2 Auxiliary crossvein present between R_{2+3} and R_4 (Fig. 83); median fork distal to radial fork ..... *C. maculatus* n.sp. / *C. falcatus* n.sp

(An undescribed female specimen from Philip Is. [Norfolk group] will also key to these species).

—— Auxiliary crossvein absent, wing unmodified; median fork proximal to radial fork (Fig. 81) 3

3 Median fork separated from radial fork by less than length of crossvein dm-cu (Fig. 84); apical third of hind tibia with row of 4–5 anterodorsal bristles ..... *C. ordinatus* Hardy

—— Median fork separated from radial fork by more than length of crossvein dm-cu (Fig. 81); apical third of hind tibia with 2 anterodorsal bristles ..... *C. hibernatus* n.sp.

4 Scutum with 3 dorsocentral bristles; stylus white ..... *C. albistylus* Hardy

—— Scutum with 4 dorsocentral bristles, with prescutellar bristles short and slender; stylus usually dark 5

5 Stigma long, nearly length of cell r_4 (Fig. 15); medial fork branching very near apex of cell dm, stem less than length of crossvein dm-cu 6

—— Stigma short, distinctly shorter than length of cell r_4 (Fig. 52); medial fork branching more distant from apex of cell dm, stem greater than length of crossvein dm-cu 7

6 Pleura pale brown ..... *C. barringtonensis* n.sp.
—— Pleura yellow, especially on anterior half ..... *C. victoriae* n.sp.

7 Acrostichal setulae absent ..... *C. athertonius* n.sp.
—— Acrostichal setulae present 8

8 Pleura nearly entirely bright yellow, or at least either with a broad yellow band or lower half of pleura yellow 9
—— Pleura mostly light to dark brown, at most proepisternum yellow above fore coxa 12

9 R_{2+3} distinctly arched or deflected around stigma (Fig. 55) 10
—— R_{2+3} nearly straight, not deflected around stigma 11

10 R_{2+3} very strongly deflected around stigma; yellow pleural band broad and long, extending to katepisternum ..... *C. inflexus* Hardy / *C. bulbosus* n.sp.
—— R_{2+3} not strongly deflected around stigma; yellow pleural band narrow and short, not extending to katepisternum ..... *C. macalpinei* n.sp.

11 Tip of stylus dark; scutum dark ..... *C. lobatus* n.sp.
—— Tip of stylus pale; scutum with pale vittae between postsutural supra-alars and dorsocentral bristle ..... *C. campbelli* (Paramonov)

12 Stylus (segments 8–10) shorter than postpedicel ..... *C. globosus* n.sp.
—— Stylus (segments 8–10) subequal to or longer than postpedicel 13

13 R_{2+3} nearly straight, sometimes only slightly deflected around stigma 14
—— R_{2+3} distinctly arched or deflected around stigma ..... *C. malleolus* n.sp. / *C. oreas* n.sp.

14 Fore coxa nearly white, in strong contrast to thorax; wing and cell r_1 very narrow; dorsolateral margin of sternite 7 straight ..... *C. orientalis* n.sp.
—— Fore coxa pale but not strikingly bright; wing and cell r_1 not obviously narrowed; dorsolateral margin of sternite 7 concave, with posterodorsal corner extended sharply upright (Fig. 37) ..... *C. attenuatus* n.sp.

Ceratomerus campbelli species-group

This unique species group is characterized by either a long comb of setae or three long spatulate processes on the anal lobe of the male wing, and the highly contorted and modified male midleg. Four species are included in this group, and together appear to be most closely related to the *C. paradoxus* group of southern Chile.

Ceratomerus athertonius n.sp.

Figs. 1, 2, 9–11, 17, 18, 28, 124

Type material. HOLOTYPE ♂, "AUST: N.QLD[Northern Queensland] 31.6 km up Mt. Lewis Rd., 1000 m/ 16.iv.1994, cascading/ creek, B.J. Sinclair/ 16°36'S 145°16'E"; "HOLOTYPE/ *Ceratomerus*/ *athertonius*/ Sinclair [red label]" AMS K175239. PARATYPES: **Queensland**: 2♂♂, 8♀♀, same data as holotype (AMS, CNC); 3♀♀, same locality as holotype, 21–22.iv.1994 (ZFMK); 2♂♂, 3♀♀, 4 km up Mt. Edith Rd, 800 m, Danbulla SF, 17°05'S 145°33'E, Ck, 22.iv.1994, BJS; 2.4 km up Mt. Edith Rd, 700 m, Danbulla SF, 27.iv.1994, 17°05'S 145°33'E, sandy str., BJS (AMS); 2♂♂, 11♀♀, 4 km up Mt. Edith Rd, 800 m, Danbulla SF, 17°05'S 145°33'E, MT across Ck, 22–27.iv.1994, BJS (ANIC, AMS, CNC); 3♀♀, Mt. Edith, 4–7 m off Danbulla Rd, 27.iv.1967, DHC (ANIC).

Diagnosis. Males readily recognized by the highly modified midlegs and long spatulate processes projecting from the anal lobe of the wing. Females are separated by lacking acrostichals, dark stylus, and pale to dark coloured pleura with at least the laterotergite and meron darkened.

Description. Wing length 3.2–3.4 mm.

Male. *Head* dark brown, face with white pruinescence, lacking setulae; ocellar triangle with 2 long, divergent bristles, inserted between ocelli; postocellar bristle short, one-half length of ocellar bristle; 3 pairs of long vertical bristles, shorter than ocellar bristles; postocular bristles very short, slender, overlapping less than one-fifth of eye. Antenna long, with scape subequal to height of eye; pedicel oval with posterior fringe of setae; scape sparsely covered by setulae, with 2 long, dorsal setae and 1 long, ventral seta. Postpedicel 1.3× longer than scape, covered by long, dense pruinescence, basal half rectangular; apical half strongly differentiated from base, tapered to short three-segmented stylus, one-third length of postpedicel; segment 8 not longer than wide; stylus concolorous with remaining antenna. Base of labrum lacking dorsal process; palpus

yellow, long and slender, one-fourth length of labrum, with lateral row of short, dark setae and stout, subapical seta; prementum with short setae only.

Thorax. Mesonotum, postnotum, laterotergite, and meron dark; remaining pleura, lateral margin of scutum, postpronotal lobe, and postalar yellowish-brown. Acrostichals absent; 4 dc, first and fourth bristles short and slender; 1 pprn; 1 presut spal; 1 npl; 2 psut spal, upper short and slender; 1 slender, short pal; 2 sctl; numerous setulae scattered on scutum, particularly among dc. Antepronotum with 2 long, lateral setae.

Wing (Fig. 9). Posterior margin with strongly sclerotized, triangular prolongation, lined with long setulae; projection bearing 3 long, narrow processes, with dilated or spatulate tips (Fig. 11); wing stem with long, stout setae. Stigma at apex of cell r_1 broad, dark, remainder of wing infuscate; single long costal seta; costal margin with unmodified setulae. R_{4+5} acutely forked; auxiliary crossvein between R_{2+3} and R_4 lacking; cell dm trapezoidal; medial fork petiolate, proximal to radial fork by slightly less than length of R_4. Halter with dark knob and white shaft.

Legs. Coxae yellow, concolorous with pleura; fore femur yellow, apex of mid and hind femur dark; tibiae with yellow dorsal margin; remaining segments dark. Fore coxa more than twice length of mid and hind coxae combined; apical third concave with inner tuft of stout setae and pair of long, wavy, sclerotized processes. Fore trochanter not lengthened, bearing row of 3–4 long, inner setae. Fore femur with pv row of very long, stout setae, more than twice width of femur; basal half with 5 widely spaced av setae, basal seta projecting obliquely; mid-length with irregular row of long anterior setae, becoming more stout apically. Fore tibia shorter than femur, apex not dilated with anteroapical comb; pv margin with row of long erect setae, length nearly twice width of tibia. First tarsomere slightly shorter than fore tibia, with 2 long ventrobasal setae; distal 4 tarsomeres longer than first tarsomere; fifth tarsomere dorsoventrally flattened.

Mid coxa with stout anterior seta. Basal two-thirds of mid femur strongly swollen, with pv tooth; av and pv margins with long stout setae, less than basal width of femur; basal third with anterior, spine-like seta; apical third of femur narrow, with long anterior setae (Fig. 1). Mid tibia shorter than femur, with concave ventral margin; apical half expanded; pv margin with row of stout setae, slightly longer than width of tibia, and short basal hooked process; base with long projecting lobe, base of lobe surrounded by series of short, convoluted lobes (Fig. 2). First tarsomere thin, longer than femur and tibia combined; apex with pair of ventral bristles; fifth tarsomere somewhat flattened.

Hind coxa bearing unmodified setae. Hind femur less than twice length of fore femur; base with pv oval zone, devoid of setae, with fringe of 7 long setae; mid-length with row of slender, ventral setae; lacking preapical dorsal bristle. Hind tibia longer than femur, apex dilated, bearing posteroapical comb; 4 ad bristles and 2 dorsal bristles on apical half. Hind tarsomeres longer than tibia; first tarsomere with 1 erect, ventral seta near base; pv margin with erect setae.

Abdomen. T1 pale brown; T2–6 dark brown, with long slender setae, especially on posterior margin; S1–6 yellow; T7 light brown, posterior margin membranous, lacking long posterior setae; S7 slightly longer than preceding sternite, anterolateral margin produced anteriorly, fused to S8; T8 one-fifth length of sternite, expanded laterally bearing long setae.

Terminalia (Fig. 17). Hypandrium with posterior flap-like process; paired articulated, curved postgonites projecting obliquely near apex of phallus. Apex of phallus with pair of sickle-shaped appendages arching posteriorly between postgonites. Epandrium with 1 very long stout seta on ventrolateral margin; epandrial lobe long, tapered, bearing 4 broad, peg-like lateral setae. Bacilliform sclerite broad, separate from epandrium. Surstylus short, round, projected posteriorly, little longer than wide, bearing marginal setulae. Cercus short, fleshy, apex acute, expanded laterally around anus; posterior surface well sclerotized.

Female. Similar to male except as follows: postpedicel slightly longer than scape; segment 8 1.5× longer than wide; palpus brown; mesonotal bristles long and stout; occasionally pleura entirely brown; wing (Fig. 10) lacking posterior projection and appendages, venation unmodified; cell dm rectangular; medial fork with short petiole, basal to radial fork by nearly length of R_4. Legs lacking modified appendages and setae; apex of fore tibia not expanded. Mid tibia with 1 long ventral, 1 ad and 1 pd apical bristle; 1 ventral and 1 ad bristle at mid-length; basal third with 1 ad and 1 pd bristle. Apical segments retracted into segment 7; posterior margin of T7 with narrow, yellowish-brown extension, bearing posterior fringe of setae; lateral margin of S7 straight. Terminalia (Fig. 18): posterior margin of T8 membranous, with dense fringe of long setae along lateral margin; pair of flat lateral sclerites extend into segment 7 from anterior margin of T8; S8 with ventral setulae; posterior margin invaginated, forming internal plate. T10 split medially into pair of rectangular sclerites, bearing double row of spine-like setae along posterior margin. Cercus bearing row of similar setae, with short, slender marginal setae. Spermathecal receptacle oval, with short, wide neck.

Distribution. This species is known only from the Atherton Tableland and Mt. Lewis of northern Queensland from 800 to at least 1000 m (Figs. 28, 124).

Etymology. Named in reference to the Atherton Tablelands where the first specimens of this species were taken by Dr D.H. Colless.

Ceratomerus barringtonensis n.sp.

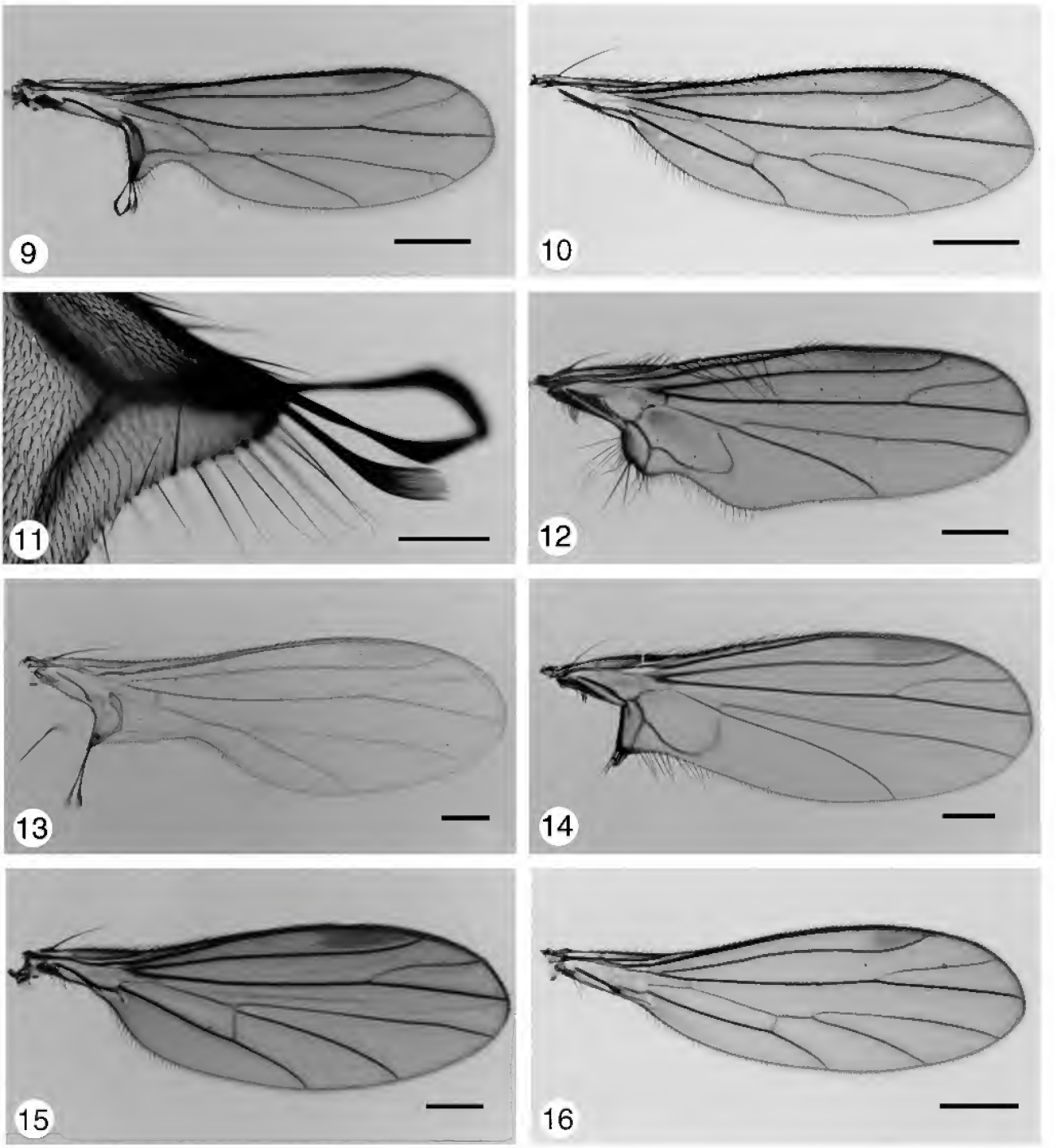
Figs. 3, 4, 12, 19–21, 28

Type material. HOLOTYPE ♂, "AUST: NSW[New South Wales]: Barrington/ Tops NP, Williams R./ 21.i.1995, 480 m/ rainfor., BJ Sinclair"; "HOLOTYPE/ *Ceratomerus/ barringtonensis/* Sinclair [red label]" AMS K175240. PARATYPES: **New South Wales**: 3♂♂, 1♀, same data as holotype (AMS, ZFMK); 4♂♂, same locality as holotype, 19.xii.1993 (CNC, ZFMK); 1♀, Gloucester Tops, *Nothofagus*, 1280 m, MT, 4–30.xii.1988, DJB (AMS).

Diagnosis. Males are readily recognized by the greatly swollen mid femur and truncate anal lobe of the wing, bearing long, wavy, slender setae. Females are distinguished by the long stigma, short base of the medial fork, yellow-coloured pleura, with brown smudges and dark-tipped stylus.

Description. Wing length 3.5–3.8 mm, similar to *C. athertonius* except as follows:

Male. *Head*. Postocellar bristles one-third length of ocellar bristles; postocular bristles short, slender, overlapping less than one-third of eye. Antenna long, with scape slightly



Figs. 9–16. Wings of *Ceratomerus*. 9–11, *C. athertonius*: 9, male; 10, female; 11, spatulate wing setae, male. 12, *C. barringtonensis*, male. 13, *C. campbelli*. 14–15, *C. victoriae*: 14, male; 15, female. 16, *C. attenuatus*, male. Scale bars = 0.5 mm, except Fig. 11 where scale bar = 0.2 mm.

longer than height of eye; scape with many dorsal setulae; three-segmented stylus one-half length of postpedicel; segment 8 not longer than wide; apical two-thirds of stylus dark. Palpus brown, short and slender, with several long, dark setae; prementum with 2 pairs of long, erect setae.

Thorax. Mesonotum and postnotum dark, lacking dorsal stripes; postpronotal lobe yellowish-brown, pleura yellow with brown smudges on lower margins of sclerites. Acrostichals in alternating single row of short setulae to prescutellar depression, posterior half directed anteriorly; 4 dc, posterior dc short and slender; lower psut spal near wing base.

Wing (Fig. 12). Anal lobe truncate, bearing pair of long, stout setae, and 6–12 pairs of long, wavy lateral setae longer than costal seta; posterior margin lacking incision, with 5–6 stout setae on wing stem. C with 16 closely spaced, long dorsal setae on upper surface between tip of Sc and R_1, shorter than costal seta. Cell dm oval; medial fork with petiole lacking or very short, proximal to radial fork by more than length of R_4. Halter with dark knob.

Legs. Coxae concolorous with pleura, hind coxae somewhat darker; ventral margin of femora yellowish brown, upper surface light brown; remaining leg segments

dark. Inner margin of fore coxa concave, with anterior row of long setae near mid-length; basal third with transverse band of fine, wavy setae. Fore trochanter unmodified. Fore femur somewhat inflated, slightly sinuous, inner margin flat lacking setae; posterior margin with single row of short setae along entire length; 1 long stout seta at base, length twice width of femur; av row of setae sinuous, apically increasing in length to greater than width of femur; basal third with biserial row of pv setae, outer row longer than width of femur; 1 long, erect preapical dorsal seta; apical fourth with ad patch of long setae. Fore tibia shorter than femur, cylindrical, with partial subapical constriction; basal half with long av and ad setae, longer than width of tibia; distal third with short, dense setae; anteroapical comb on apex of anteriorly deflected tip. First tarsomere three-quarters length of fore tibia, cylindrical; long ventral setae, longer than width of tarsus; 1 erect ventral seta at base.

Mid coxa with slender setae. Mid femur greatly swollen, strongly arched, with large curved, ventral tubercle; tubercle with 2–3 long ventral setae and 3 stout subapical setae, terminating in round, subapical finger-like process; basal third with short setae; apical fourth with short, tapered, black pv appendage (Fig. 3). Mid tibia two-thirds length of femur, laterally expanded, with deep concave ventral surface; pv margin with row of long setae, longer than width of tibia; anteroapical margin with broad lobe extending beyond base of tarsomere, lateral margin with row of more than 10 short, curved setae; av margin of basal half with several short, convoluted lobes, pair of erect, stout setae, and comb of short setae; 1 long, erect pd apical seta (Fig. 4). First tarsomere sinuous, nearly twice length of tibia; subbasal lobe densely clothed in microtrichia; anterior and posterior margins with long, curved setae, longer than twice width of tarsus, longest at mid-length; first tarsomere shorter than remaining 4 tarsomeres.

Hind femur bow-legged, nearly twice length of fore femur, bearing long av and pd setae on apical third; 1 erect, subapical dorsal seta. Hind tibia with ad and av row of long, erect setae, nearly 3× width of tibia; basal fourth with long, erect dorsal seta. Hind tarsomeres longer than tibia; tarsomeres 1–3 clothed in long erect setae; fifth tarsomere dorsoventrally flattened.

Abdomen. Sclerites paler than thorax, with long, stout setae along posterior margin of T1–6; posterior margin of T7 with broad U-shaped membranous region; T8 very slender, one-sixth length of sternite, lateral margin expanded.

Terminalia (Fig. 19). Hypandrium with posterior broad flap, folded anteriorly, bearing crown of long setae; paired articulated postgonites flanking phallus, project dorsally, apex attenuated. Phallus flattened, apex truncate with lateroapical sickle-shaped extensions curving around anterior margin of postgonites. Epandrium with 1 very long and 3–4 shorter, stout setae on ventrolateral margin; pair of round lobes flanking base of surstylus: anterior lobe with apical setulae, posterior lobe with crown of very stout, flattened setae. Bacilliform sclerite broad, fused to epandrium near base of cercus; small lobe from bacilliform sclerite at base of anterior epandrial lobe. Surstylus fin-shaped, tapered, bearing lateral setulae; base with 4 long setae. Cercus short, fleshy, apex acute, expanded laterally around anus; posterior surface well sclerotized.

Female. Similar to male and female of *C. athertonius* except as follows: postpedicel short, subequal in length to scape; wing lacking posterior modification and setae; cell dm rectangular; medial fork with short petiole, basal to radial fork by more than length of R_4. Legs lacking modified appendages and setae; apex of fore tibia slightly expanded. Mid tibia with 1 ventral bristle at mid-length. Hind tibia with 3 ad bristles and 1 dorsal bristle. Terminalia (Fig. 21): median region of T8 with deep U-shaped weakly sclerotized zone; fringe of long setae. S8 subtriangular in lateral view. Spermathecal receptacle spherical, with short neck; base of spermathecal duct pigmented (Fig. 20).

Distribution. This species is known only from two localities in Barrington Tops National Park (Fig. 28).

Biology. Most adult specimens were collected from the underside of somewhat flattened emergent rocks in the Williams River located at Rocky Crossing. This river valley is surrounded by subtropical rainforest. A single specimen was collected at 1280 m in *Nothofagus* forest.

Etymology. Named in reference to type locality.

Ceratomerus campbelli (Paramonov)

Figs. 5, 6, 13, 22–24, 28, 88

Tomia campbelli Paramonov, 1961: 101.

Type material. HOLOTYPE ♂, "Interview R. area/ N of Pieman R., Tasm./ 31 Dec. 1953/ T.G. Campbell"; "Tomia/ campbelli/ Paramonov/ HOLOTYPE ♂ [red label]"; "Paramonov det./ Tomia/ campbelli/ gen et sp. nov./ Typus ♂ [hand written]" (ANIC).

Additional material. Tasmania: 1♀, nr Candle Mtn, Pencil Pine Ck, 800 m, high woodland, pans, 30.i.1989; 2♂♂, 4♀♀, Hartz Mtns NP, nr Keogh Falls, 23.i.1989, rock seep.; 1♀, Frodshams Pass nr Mt. Wedge, 4–5.ii.1989, rainfor., y.pans; 1♂, Mt. Bobs Range, Pine Lk., 680 m, W. Hartz Mtns, 23.i.1989, wet heath (AMS); 1♀, Hellyer Gorge, 2.ii.1967 (ANIC); 3♂♂, 1♀, Mt. Bobs Range, nr Pine Lk., 700 m, 23.i.1989, rainfor., y.pans (AMS, CNC, ZFMK).

Diagnosis. This is the largest sized species in Tasmania, with males readily recognized by the long highly modified midlegs and processes projecting from the anal lobe of the wing. Females are separated by pale-coloured pleura and white-tipped stylus.

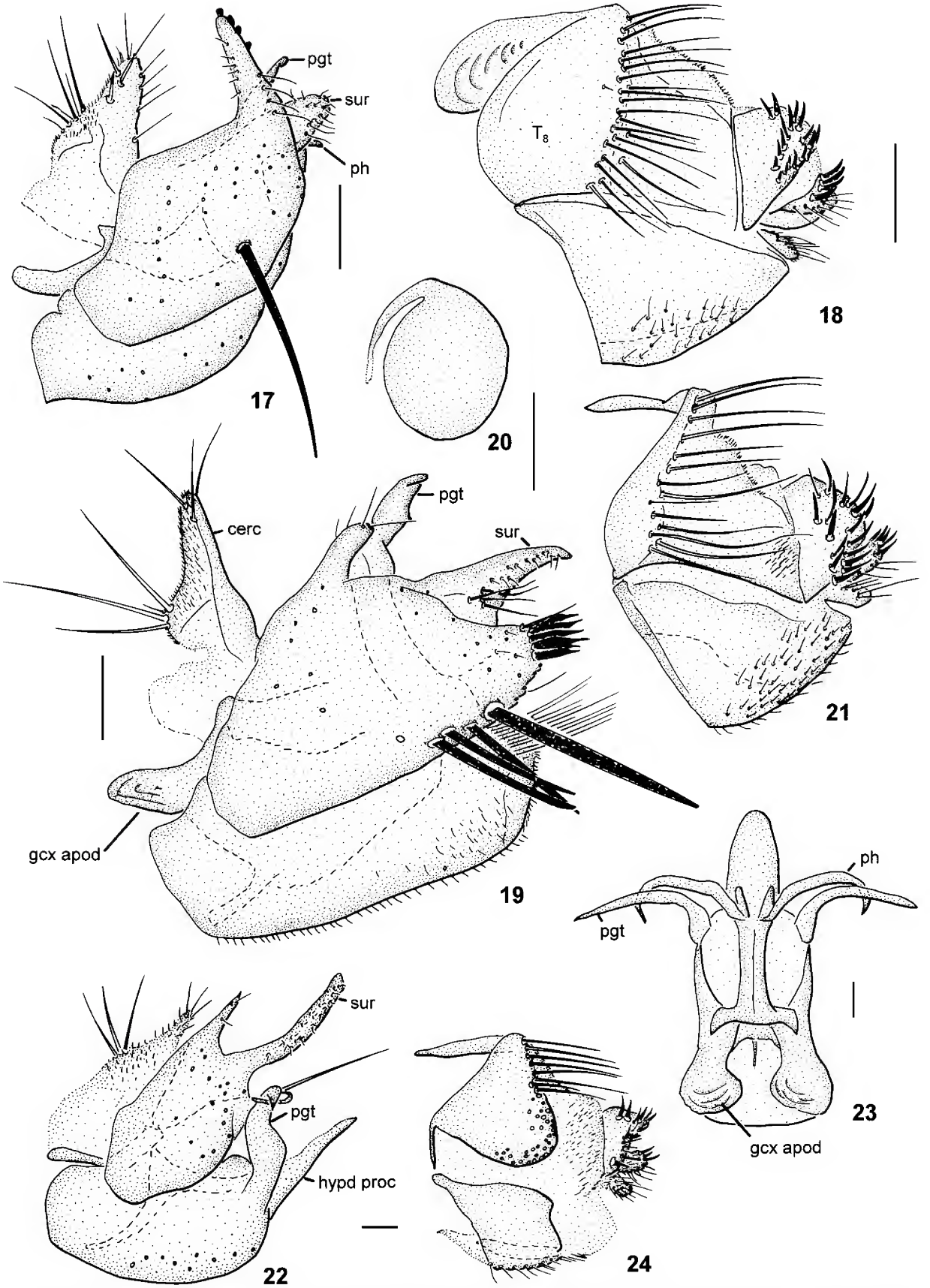
Description. Wing length 4.7–5 mm, similar to *C. athertonius* except as follows:

Male. *Head*. Postocellar bristles short, one-third length of ocellar bristles; postocular bristles short, slender, overlapping less than one-third of eye. Antenna long, with scape subequal to half length of labrum; three-segmented stylus subequal to half length of postpedicel; segment 8 4–5× longer than wide; apical two-thirds of stylus white. Palpus brown, one-third length of labrum, with several long, dark setae.

Thorax. Mesonotum and postnotum dark, with 2 wide, reddish-brown stripes on either side of dc; pleura, postpronotal lobe pale. Two long anterior acrostichals, followed by alternating single row of short setulae to prescutellar depression, directed anteriorly; 4 dc, posterior dc short and slender; 2 psut spal, lower near wing base; numerous setulae scattered on scutum, particularly on pprn, among dc and npl.

Wing (Fig. 13). Wing stem with long, undifferentiated setae; cell dm triangular. Halter with dark knob.

Legs. Coxae concolorous with pleura. Fore coxa armed on inner margin one-third before apex with tuft of stout setae and pair of long, sclerotized processes similar to a collapsed sac (Fig. 88); distal to process, inner surface deeply concave. Fore



Figs. 17–24. Terminalia of *Ceratomerus*. 17–18, *C. athertonius*: 17, male, lateral view; 18, female, lateral view. 19–21, *C. barringtonensis*: 19, male, lateral view; 20, spermatheca, 21, female, lateral view. 22–24, *C. campbelli*: 22, male, lateral view; 23, hypandrium and phallus, dorsal view; 24, female, lateral view. Scale bars = 0.1 mm. Abbreviations: *cerc*, cercus; *gcx apod*, gonocoxal apodeme; *hypd proc*, hypandrial process; *pgt*, postgonite; *ph*, phallus; *sur*, surstylus; *T*, tergite.

trochanter equal to one-third of fore coxa, bearing row of 4–5 short setae. Fore femur with very long, stout basal seta; mid-length of anterior region with patch of long, erect setae; pv region with row of stout setae, increasing in length apically. Fore tibia equal in length to femur + trochanter, apex dilated covered with rows of short setae and bearing anteroapical comb; basal half of anterior region with row of long, erect setae; pv region with row of stout setae, increasing in length apically. First tarsomere slightly shorter than fore tibia, with pd apical row of 5–6 stout setae.

Mid coxa with stout lateral seta and transverse row of setae on anterior face. Basal half of mid femur strongly thickened, with large av tubercle; ventral region of basal half armed with 2 long, stout setae and wide, flattened, curved seta; apical half with ad row of stout setae; ventral region of apical half with 2 long setae and short, flattened, finger-like process (Figs. 5, 6). Mid tibia shorter than femur extremely modified by series of variously ornamented processes and setae. First tarsomere longer than remaining 4 tarsomeres.

Hind coxa with transverse row of setae on anterior face. Hind femur twice length of fore femur, bearing row of 7–9 long, flattened pv setae near mid-length; preapical seta, long, stout, projecting perpendicular to posterior surface. Hind tibia longer than femur, apex dilated, bearing posteroapical comb; subapical posterior region with shallow notch; ad region with 1 subapical seta and 2 setae on basal half; 1 erect dorsal seta near mid-length.

Abdomen brown, with long, stout setae along posterior margin of T1–6; T7 membranous.

Terminalia (Figs. 22, 23). Hypandrium with posterior flap-like process; paired articulated, curved postgonites projecting laterally near apex of phallus. Apex of phallus with laterally projecting sickle-shaped appendages which arch anteriorly beneath postgonites. Epandrium with short pointed lobe projected anterior to surstylus. Surstylus slender, arched dorsally, parallel-sided with rounded apex, bearing setulae. Cercus short, fleshy, apex acute, expanded laterally around anus.

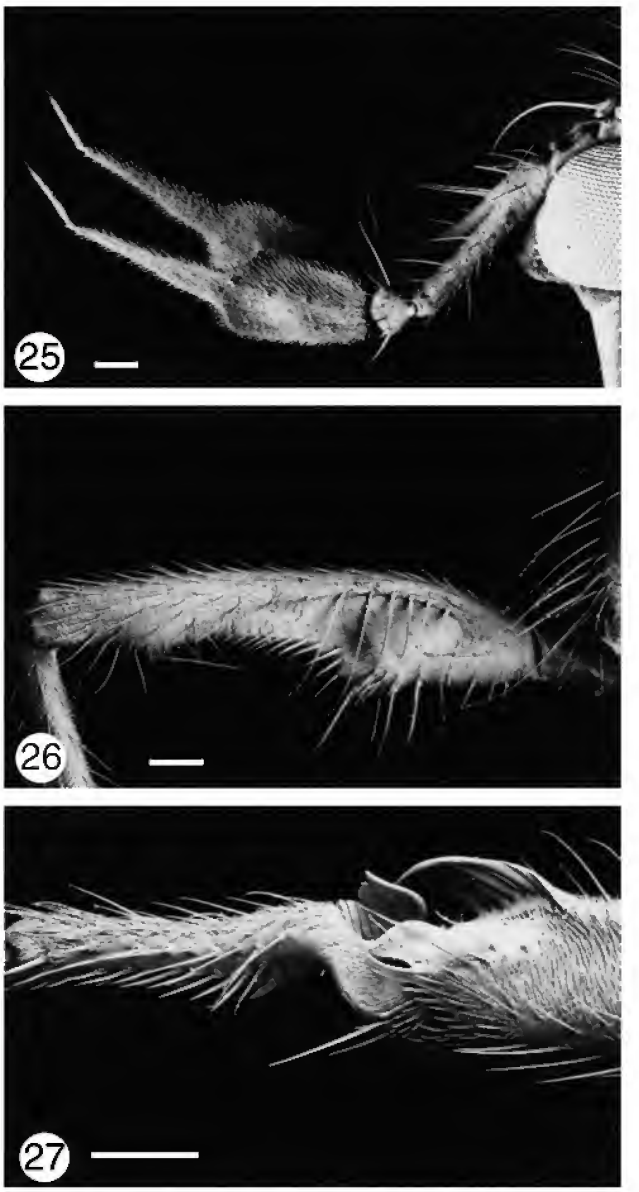
Female. Similar to male and female of *C. athertonius* except as follows: wing lacking posterior incision and appendage; medial fork with short petiole, basal to radial fork by slightly more than half length of R_4. Apex of fore tibia slightly expanded. Posterior fringe of setae on T7 restricted to lateral margins. Terminalia (Fig. 24): T8 largely membranous, with dense fringe of setae along lateral margins; S8 with median stripe of setae. T10 bearing short, spine-like setae; cercus short with small apical spine-like setae. Spermathecal receptacle slightly oval, with duct attached directly, lacking pigmented ridge or neck-like extension.

Distribution. This species is restricted to the moist, higher elevations of the western half of Tasmania (Fig. 28).

Ceratomerus victoriae n.sp.

Figs. 7, 8, 14, 15, 25–28, 30–33

Type material. HOLOTYPE ♂, "AUST: VIC[toria]: 9 km N/ Warburton, Cement Ck./ 1–3.xii.1994/ B.J. Sinclair/ ex. *Nothofagus* for."; "HOLOTYPE/ *Ceratomerus*/ *victoriae*/ Sinclair [red label]" AMS K175241. PARATYPES: **Victoria**: 15♂♂, 10♀♀, same data as holotype (AMS, ANIC, CNC, ZFMK); 2♂♂, 3♀♀, Acheron Ck, 29 km from Warburton, 1–3.xii.1994, y.pans, BJS, DJB; 4♂♂, Cement Ck, 800 m, rainfor., y.pans, 1–3.xii.1994, DJB; 2♀♀, Errinundra Plateau, Result Ck, & Gap Rd, 920 m, rainfor., y.pans, 6.xii.1994, DJB; 1♂, 3♀♀, Otway Ra., SE Beech For., Beauchamp Falls, y.pans, 350 m, 4–5.xii.1994, DJB (AMS); 1♀, Acheron Gap, 15 km NNE Warburton, MT, 830 m, 6–12.xii.1990, D. Pollock, L. Reichert; 1♂, Cement Ck, 27.x.1961, DHC; 1♀, Cement Ck, 670 m, *N. cunninghamii*, 10–17.i.1980, A. Newton, M. Thayer (ANIC); 1♂, Cement Ck, 27.iii.1972, A. Neboiss (MVM); 4♂♂, 2♀♀, Errinundra Plateau, Gap Rd, Result Ck Falls, 6–7.xii.1994, BJS (MVM, ZFMK); 3♂♂, 2♀♀, Otway Ra., Beauchamp Falls, *Nothofagus*, 3.xii.1994, BJS (ZFMK); 2♂♂, 4♀♀, Otway Ra., Melba Gully SP, temperate rainfor., ck, 4.xii.1994, BJS (CNC).



Figs. 25–27. Scanning electron micrographs of male *Ceratomerus victoriae*: 25, head, lateral view; 26, fore femur, anterior view; 27, fore first tarsomere and apex of tibia, posterior view. Scale bars = 0.1 mm.

Diagnosis. Males are readily recognized by highly modified midlegs and anal lobe of the wing acutely produced, bearing many stout setae. Females are separated by the yellow-coloured pleura, short base of the medial fork, and dark-tipped stylus.

Description. Wing length 4.2–4.5 mm, similar to *C. athertonius* except as follows:

Male. *Head*. Postocellar bristles one-third length of ocellar bristles; vertical bristles somewhat shorter than ocellar bristles; postocular bristles short, slender, overlapping one-third of eye.

Antenna long, with scape slightly longer than height of eye (Fig. 25). Postpedicel 1.6× longer than scape; palpus yellow, short and slender, one-fourth length of proboscis, with several long, dark setae; prementum with 1 pair of erect setae.

Thorax. Mesonotum and postnotum dark, lacking dorsal stripes; postpronotal lobe brown, pleura yellow. Acrostichals in alternating single row of short setulae to prescutellar depression, directed anteriorly; 4 dc, posterior dc short and slender; 2 psut spal, lower near wing base; numerous setulae scattered on scutum, particularly around presut spal and dc.

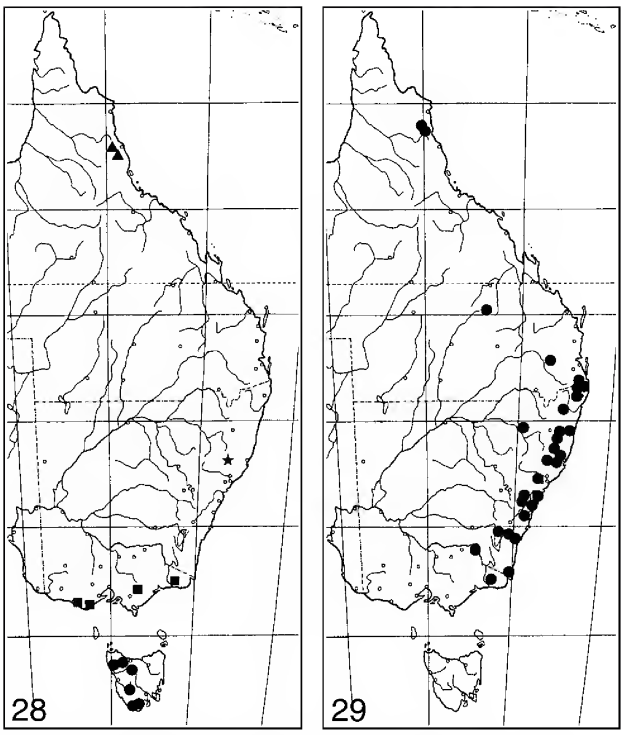
Wing (Fig. 14). Anal lobe acutely produced, bearing more than 15 short, stout setae; posterior margin lacking incision, with 3 stout, flattened setae on wing stem. C with 12 widely spaced, long dorsal setae on upper surface between tip of Sc and R_1, longer than costal seta. Cell dm oval; medial fork proximal to radial fork by more than length of R_4, usually with very short petiole or stem. Halter with dark knob.

Legs. Coxae concolorous with pleura, hind coxa somewhat darker; base and inner margin of femora yellowish brown, dark apically; remaining leg segments dark. Inner margin of fore coxa gradually tapered, parallel-sided, with anterior row of long setae on apical half and inner subapical patch of fine setae; apical third with long stout seta, half length of coxa on near inner ventral margin. Fore trochanter unmodified. Fore femur swollen, inner margin concave on basal two-thirds; upper edge of depression with row of 7 long, ventrally directed setae, longer than width of femur (Fig. 26); av margin with row of stout, black setae, decreasing in length apically, longest on apex of ventral swelling; apical fourth with ventral swelling with av fringe of long setae and 1 ventral, near horizontal projecting stout seta. Fore tibia longer than femur + trochanter, with mid-length constriction or weakening; distal half with anterior and posterior surfaces concave, clothed in short appressed setae; apex with pd comb of tightly appressed, arched, stout setae; anteroapical comb present. First tarsomere less than half length of fore tibia, with deep basal notch; short, arched comb opposing tibial comb (Fig. 27); 1 erect, ventral seta at base; distal 4 tarsomeres nearly twice length of first tarsomere.

Mid coxa with slender setae. Mid femur thickened, strongly arched, with large curved, ventral tubercle; tubercle lined with long ventral setae, terminating in pointed, subapical finger-like process; basal third with long av and pv setae, longer than width of femur; apical fourth with short, slender, black pv appendage (Figs. 7, 8). Mid tibia two-thirds length of femur, laterally expanded, with deep concave ventral surface; pv margin with row of long setae, longer than width of tibia; anteroapical margin with broad lobe extending beyond base of tarsomere; av margin with several short, rounded lobes; 2 long, erect ad setae. First tarsomere 1.3× longer than tibia; base with pv row of 3 stout setae; apical half with anterior row of stout, curved, flattened setae; basal half with long, anterior and ad setae, longer than width of tibia; first tarsomere nearly subequal in length to remaining 4 tarsomeres.

Hind femur less than twice length of fore femur, bearing av patch of curled, golden setulae; basal third with row of 3–5 long, erect setae; 1 erect, subapical dorsal seta. Hind tibia longer than femur, apex not dilated, bearing posteroapical comb; 4 erect ad setae and 2 erect dorsal setae on apical half. Fifth tarsomere not strongly flattened.

Abdomen. Tergites concolorous with thorax, with long, stout setae along posterior margin of T1–6; sternites pale brown; T8 very slender, one-sixth length of sternite, lateral margin expanded.



Figs. 28–29. Known distribution of species of *Ceratomerus* (eastern Australia). 28, *C. athertonius* ▲, *C. barringtonensis* ★, *C. campbelli* ●, *C. victoriae* ■. 29, *C. orientalis*.

Terminalia (Figs. 30, 31). Hypandrium with posterior broad flap, folded anteriorly, bearing crown of long setae; paired articulated postgonites flanking phallus, projecting dorsally, apex forked. Phallus flattened, apex truncate with lateroapical sickle-shaped extensions curving around anterior margin of postgonites. Epandrium with 1 very long, stout seta on ventrolateral margin; pair of round setose lobes flanking surstylus, with anterior lobe bearing radiating crown of thickened setae, posterior lobe bearing crown of very stout, flattened setae. Bacilliform sclerite broad, fused to epandrium near base of cercus; small, round lobe from bacilliform sclerite near anterior epandrial lobe. Surstylus fin-shaped, tapered, bearing lateral setulae; base with pair of long setae. Cercus short, fleshy, apex acute, expanded laterally around anus; posterior surface well sclerotized.

Female. Similar to male and female of *C. athertonius* except as follows: postpedicel short, subequal in length to scape; palpus dark. Medial fork with very short petiole, basal to radial fork by more than length of R_4 (Fig. 15). Apex of fore tibia slightly expanded. Mid tibia with long, erect ventroapical seta; 1 erect ventral seta at mid-length; basal third with ad and pd seta. Posterior margin of T7 with complete fringe of golden setulae. Terminalia (Fig. 32): S8 subtriangular in lateral view. Spermathecal receptacle oval, flattened, with distinct wide neck (Fig. 33).

Distribution. This species is known from several isolated remnant patches of *Nothofagus* rainforest in Victoria (Fig. 28). These localities are often in deep, cool ravines, well shaded and consequently the stream temperatures are also fairly cool.

Biology. Relatively large numbers were swept above Cement Creek from the overhanging frons of tree ferns.

Adults were also aspirated from the under side of emergent rocks that had formed small, dark enclaves above the water surface. Adults appeared to seek these hiding spots, which was identical to behaviour observed for *C. barringtonensis*.

Etymology. Refers to the state where the material for this species was collected.

Ceratomerus inflexus species-group

This Australian species group is characterized by laterally inflated male terminalia, where the epandrial lamellae are normally highly convex, R_{2+3} is slightly to strongly deflected and arched around the stigma, and antennal segment 8 (second flagellomere) is much longer than wide. The relationship of this group remains doubtful, although appearing to be the sister group to all remaining Australian species exclusive of the *C. ordinatus* group.

Ceratomerus attenuatus n.sp.

Figs. 16, 35–38, 43

Type material. HOLOTYPE ♂, "AUST[ralia]: NSW[New South Wales]: Dorrigo NP/ Wonga Walk, 700 m/ Crystal Shower Falls/ 2.iv.1995/ B.J. Sinclair"; "HOLOTYPE/ *Ceratomerus*/ *attenuatus*/ Sinclair [red label]" AMS K175242. PARATYPES: **Australian Capital Territory**: 4♂♂, 1♀, Blundells Ck, 35°22'S 148°50'E, iii., vi.1987, v.1988, DHC (ANIC). **New South Wales**: ♂, same data as holotype (AMS); 4♂♂, 3♀♀, Border Ranges NP, Brindle Ck, 1000 m, rainfor., y.pans, 25–26.i.1995, BJS (CNC, ZFMK); 1♂, Dorrigo NP, Rosewood Ck, 23.i.1995, BJS; 5♂♂, 4♀♀, Gloucester Tops, 1280 m, *Nothofagus*, MT, 19.xi–4.xii.1988, DJB; 1♀, Styx River SF, George's Ck For. Res., Cunnawarra Ck, 31.iii.1995, BJS (AMS); 1♂, 2♀♀, nr Gloucester Tops, 1290 m, *Nothofagus*, 14–19.xi.1988, DJB (AMS, ANIC); 1♀, Monga SF, 19–24.i.1984, L. Masner (CNC). **Queensland**: ♀, Lamington NP, Green Mtns, Elabana Falls, Canungra Ck, 6.v.1994, BJS (AMS). **Victoria**: 9♂♂, 1♀, Acheron Ck, 29 km from Warburton; y.pans, rainfor. ck, 400 m, 1–3.xii.1994, DJB; 5♂♂, Burrowa-Pine Mtn NP, Bluff Ck Falls, 400 m, riverine for., y.pans, 29.xi.1994, DJB; 2♂♂, 1♀, same locality, swept over pools, 29.xi.1994, DJB; 1♂, Cement Ck, rainfor., 800 m, y.pans, 1–3.xii.1994, DJB; 6♂♂, 3♀♀, Errinundra Plateau; Bonang Ck, y.pan, 1.iv.1990, DJB; 2♂♂, 4♀♀, same locality, Result Ck; 1♂, 1♀, Errinundra Plat., Result Ck + Gap Rd., 900 m, cool rainfor., y.pans, 6.xii.1994, DJB (AMS); 5♂♂, 1♀, same locality, Cudgewa Bluff Falls, 400 m, rainfor., 30.xi.1994, BJS (CNC, ZFMK).

Diagnosis. Recognized by the very slight inflexion of R_{2+3} around the stigma, dorsolateral margin of female sternite 7 concave with posterior corner extended dorsally, and distinctive capsule-like male hypopygium with long slender cerci.

Description. Wing length 2.8–3.5 mm.

Male. *Head* dark brown, dull; upper half of face pale brown, lacking setae; lower half of face with dense white pruinescence; ocellar triangle with 2 widely spaced, long, divergent bristles, inserted anterior to lateral ocelli; postocellar bristles short, one-half length of ocellar bristles; 3 pairs of vertical bristles, shorter than ocellar bristles; postocular bristles short, slender, overlapping less than one-third of eye. Antenna with length of scape slightly more than half height of eye, with 2 dorsal setae, several lateral setulae and 1 long ventral seta; pedicel globular, with setae confined to apical fringe. Postpedicel covered by long, dense pruinescence, length slightly longer than height of head; base rectangular; apical half strongly tapered, subequal in length to base; three-segmented stylus subequal in length to postpedicel; segment 8 long, 4–5× longer than width; stylus concolorous with remaining segments. Base of labrum lacking dorsal process; palpus brown, slender, one-fourth length of labrum, with several dark setae; prementum with short setae only.

Thorax. Scutum and postnotum dark brown; pleura brown; postpronotal lobe pale; pale streak extending ventrally along proepisternum and anterior margin of anepimeron; scutum lacking vitta of pruinescence. Alternating row of short acrostichals to prescutellar depression, directed anteriorly; 4 dc, fourth dc short and slender; 1 pprn; 1 presut spal; 1 npl; 2 psut spal; 1 pal, short; 2 sctl; additional setulae lacking. Antepronotum with pair of long setae.

Wing (Fig. 16) infuscate, stigma distinct, short somewhat triangular in shape at apex of cell r_1; 1 long costal seta; costal margin with unmodified setulae; posterior margin lacking incision; posterior setal margin complete, with 3 long setae on wing stem. R_1 reaching costa before middle of wing; R_{2+3} running parallel and close to costa, slightly arched around stigma; medial fork proximal to radial fork; cell dm rectangular, slender; auxiliary crossvein between R_{2+3} and R_4 lacking. Halter with dark knob.

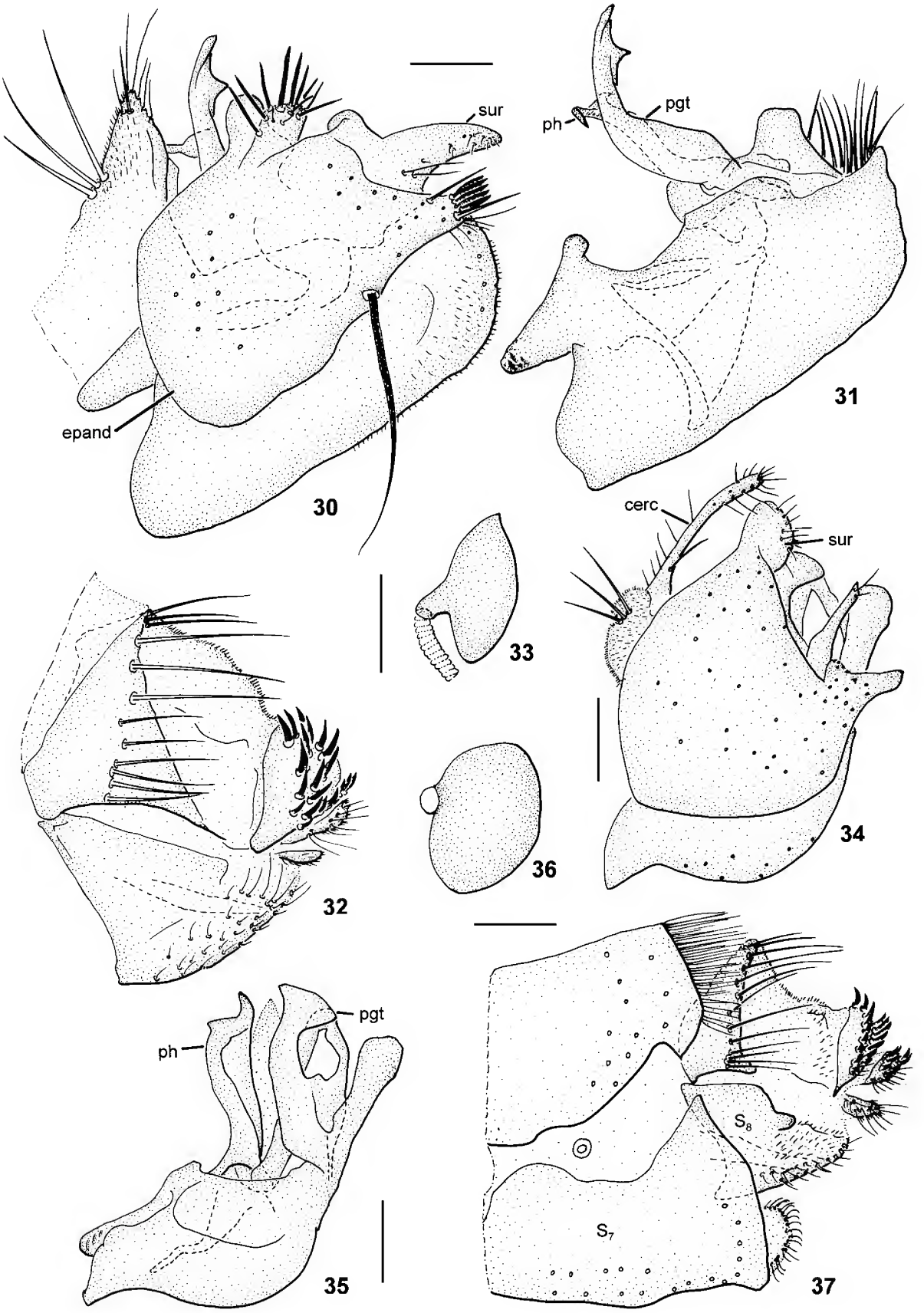
Legs. Fore and mid coxae yellow, hind coxa yellowish-brown; base of femora, especially inner margin yellow, becoming dark brown towards tip. Fore coxa slightly less than twice length of mid coxa, lacking modified setae. Fore trochanter lacking modified setae. Fore femur slightly swollen, with av row of fine setae, decreasing in length apically; 1 preapical dorsal seta. Fore tibia slightly shorter than femur; apex with anteroapical comb, not dilated. First tarsomere nearly two-thirds length of fore tibia, lacking modified setae; all tarsomeres slender.

Mid coxa lacking modified seta. Mid femur partially swollen, with pv row of short, dark setae along middle two-thirds; base with long erect pv seta; basal third with av biserial row of short dark setae (Fig. 38). Mid tibia not swollen at mid-length, with av row of short setae; pv surface with row of slender setae, shorter than width of tibia; 1 dorsal seta on basal third and 1 pd seta near mid-length. First tarsomere subequal in length to remaining 4 tarsomeres, with many erect pv setae, including long basal seta; tarsomere 5 not noticeably more flattened than on other legs.

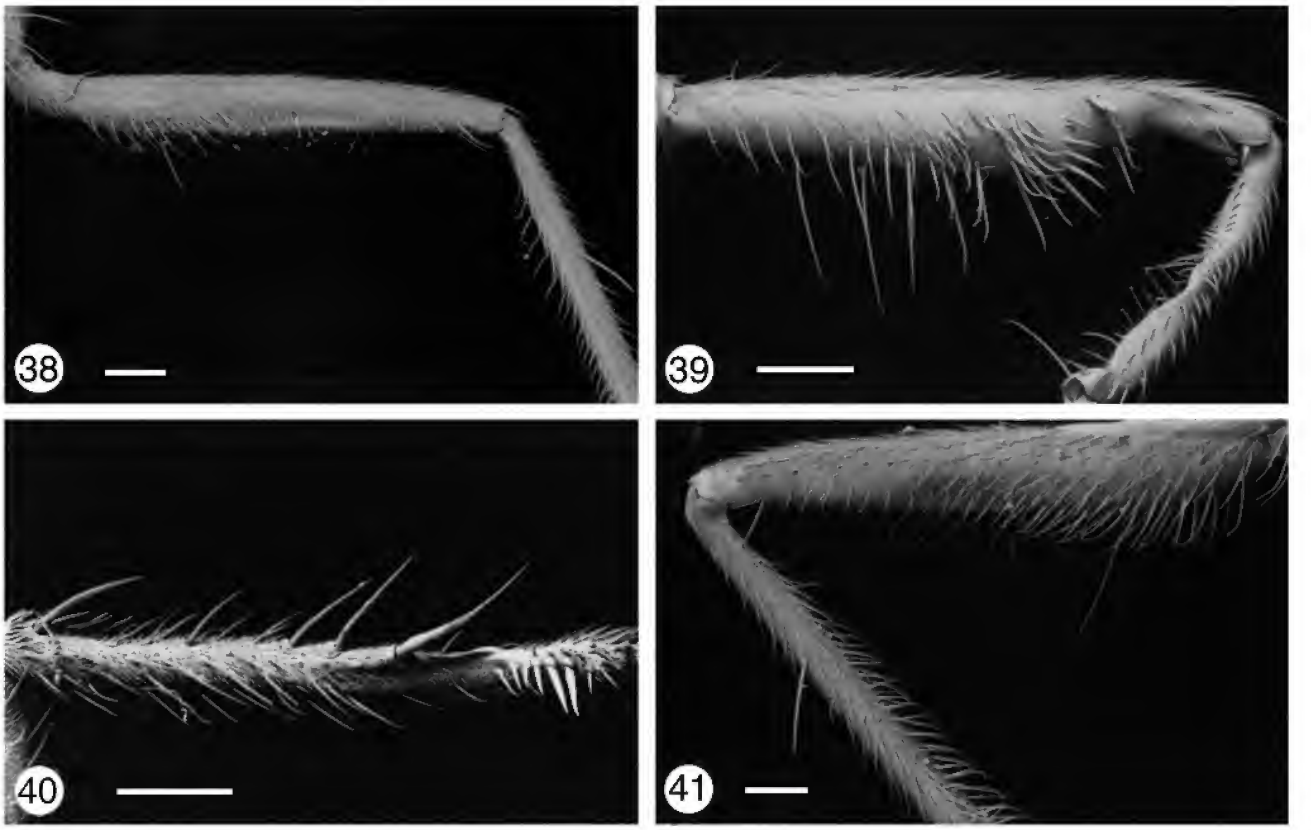
Hind coxa with unmodified setae. Hind femur straight with 1 preapical ad seta; ventral surface lacking distinct row of setae beneath. Hind tibia straight, shorter than femur, apex partially dilated, bearing posteroapical comb; pv surface lacking setae; 3 erect ad setae on apical two-thirds; dorsal margin with 2 erect setae on distal half. Hind tarsomeres longer than tibia; first tarsomere with 1 long, erect ventral seta near base.

Abdomen brown, concolorous with thorax, sclerites of segment 1–6 well sclerotized; posteromarginal setae increasing in length apically, longest on T6, where setae half width of abdomen; sternites and tergites lacking modified setae and ridges; T7 thinly sclerotized medially, lacking long posteromarginal setae; S7 only slightly longer than preceding sternite, anterolateral margin produced anteriorly; T8 bow-tie shaped.

Terminalia (Figs. 34, 35). Hypandrium convex, posterior margin produced into pair of long processes, expanded apically, nearly subequal in length to postgonites; gonocoxal apodemes developed, not projected beyond anterior margin; postgonites upright, gently arched posteriorly, fused anteriorly with pair of lateral processes (phallic), and concave median process; phallus upright, gently arched with subapical hook and arched apex. Epandrial lamella nearly circular in lateral view, forming



Figs. 30–37. Terminalia of *Ceratomerus*. 30–33, *C. victoriae*: 30, male, lateral view; 31, hypandrium and phallus, lateral view; 32, female, lateral view; 33, spermatheca. 34–37, *C. attenuatus*: 34, male, lateral view; 35, hypandrium and phallus, lateral view; 36, spermatheca, 37, female, lateral view. Scale bars = 0.1 mm. Abbreviations: *cerc*, cercus; *epand*, epandrium; *pgt*, postgonite; *ph*, phallus; *S*, sternite; *sur*, surstylus.



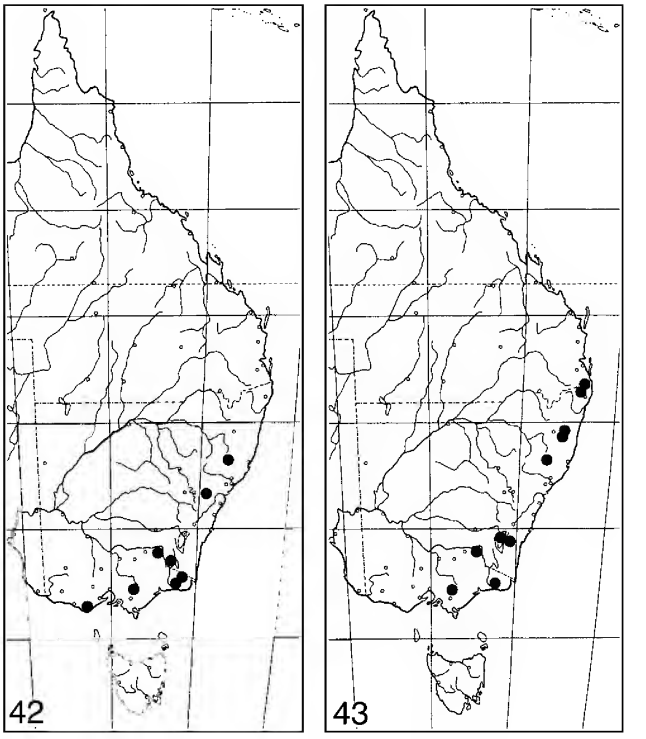
Figs. 38–41. Scanning electron micrographs of male legs of *Ceratomerus*. 38, *C. attenuatus*, midleg, anterior view. 39–40, *C. globosus*: 39, midleg, anterior view; 40, fore first tarsomere, ventral view. 41, *C. malleolus*, midleg, anterior view. Scale bars = 0.1 mm.

a partial capsule fused ventrally to hypandrium; bearing short, oblique, finger-like, posterior epandrial lobe. Surstylus short, thumb-like; inner margin with dense mat of short, stout setae; lateral margin with row of setae. Subepandrial plate narrow, extending laterally to epandrial margin; apex bearing slender process projected beyond epandrium; base of process secondarily fused to epandrium. Cercus very long and slender, sparsely clothed in setae.

Female. Similar to male except as follows: av row of setae of fore and hind femora short; mid femur slender; lacking rows of ventral setae on mid femur and tibia; mid tibia with long, erect, ad and pv apical seta; erect pv seta at mid-length. Apical segments retracted into segment 7; apical margins of segment 7 not folded inwards; posterior margin of T7 entire, with fringe of golden setulae; lateral margin of S7 concave, with pd corner extended sharply dorsally. Terminalia (Fig. 37): median region of T8 with deep U-shaped weakly sclerotized zone; fringe of long setae anterior to membranous region; anterior margin with flattened, internal, median plate. S8 triangular in lateral view, with short, rounded process; posterior margin invaginated, forming internal plate. T10 split medially into pair of rectangular sclerites, bearing double row of spine-like setae along posterior margin. Cercus bearing biserial row of spine-like setae, with short, slender marginal setae. Spermathecal receptacle oval, flattened with duct attached to broad asymmetrical neck (Fig. 36).

Distribution. This species is recorded sporadically from streams in subtropical rainforests of northern NSW and southern Queensland to gallery rainforests of Victoria (Fig. 43).

Etymology. The specific name is from the Latin *attenuatus* (drawn out or thin), referring to slender, thread-like male cercus.



Figs. 42–43. Known distribution of species of *Ceratomerus* (eastern Australia). 42, *C. globosus*. 43, *C. attenuatus*.

Ceratomerus bickeli n.sp.

Figs. 44, 100

Type material. HOLOTYPE ♂, "TAS[mania, Australia]: Frodshams Pass/ nr.Mt. Wedge;4–5.ii./ -1989; rainforest/ D.Bickel;yellowpan"; "HOLOTYPE/ *Ceratomerus*/ *bickeli*/ Sinclair [red label]" AMS K175243.

Diagnosis. Recognized by the strong inflexion of R_{2+3} around the stigma and the very long, slender posterior hypandrial processes and cerci.

Description. Wing length 3.7 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Four pairs of vertical setae, shorter than ocellar bristles; postocular bristles short, overlapping less than one-third of eye. Antenna with length of scape slightly less than height of eye; postpedicel length less than height of head; three-segmented stylus longer than postpedicel; segment 8 elongate, 4× as long as wide. Palpus brown, slender, one-sixth length of labrum.

Thorax. Upper margin of pleura brown, remaining pale brown; postpronotal lobe pale.

Wing. R_{2+3} running parallel and close to costa, strongly deflected around stigma.

Legs. Fore and mid coxae and ventral of femora pale yellow, remaining leg segments brown, darker towards tip. Fore femur slightly swollen, with av row of fine setae, decreasing in length apically; basal setae nearly subequal in length to width of femur. First tarsomere greater than half length of fore tibia.

Mid femur more strongly swollen than fore femur, with pv row of short, dark setae and 1–2 long basal setae; basal half with av brush of short dark setae, increasing in length medially. Mid tibia very slightly swollen at mid-length, with av row of short setae; pv surface with row of slender setae, longer than width of tibia; ventroapically with row of short erect setae on apical sixth; 1 ad seta on proximal half. First tarsomere ⅘ length of remaining 4 tarsomeres, with many erect pv setae.

Hind femur straight with 1 preapical dorsal and 1 ad seta; ventral surface with av row of fine setae, shorter than width of femur. Hind tibia straight, shorter than femur, apex partially dilated, bearing posteroapical comb; 2 erect ad setae at mid-length and 1 subapical ad seta; apical two-thirds with row of long, erect dorsal setae. Hind tarsomeres slightly longer than tibia.

Abdomen pale brown, concolorous with thorax, sclerites weakly sclerotized; T8 not examined.

Terminalia (based on undissected specimen) (Fig. 44). Hypandrium with pair of long, slender posterior processes, partially twisted; 1 pair of short anterior, hooked, articulated processes arched posteriorly near surstyli; postgonites arched anteriorly, flanking pair of phallic processes. Epandrial lamella greatly inflated laterally, round; fused ventrally to lateral wall of hypandrium. Surstylus finger-shaped, shorter than cercus. Cercus with broad base, with long, heavily sclerotized lateral process, similar to posterior hypandrial process.

Female. Unknown.

Distribution. This species is restricted to Tasmania (Fig. 100).

Etymology. The specific name honours Dr D.J. Bickel, who collected the holotype of this species and many other rare species from Tasmania.

Ceratomerus bulbosus n.sp.

Figs. 45, 46, 100

Type material. HOLOTYPE ♂, "TAS[mania, Australia]: nr Cradle Mtn./ Pencil Pine Ck; 800 m/ 30-i-1989; D.Bickel/ high woodlands;pans"; "HOLOTYPE/ *Ceratomerus*/ *bulbosus*/ Sinclair [red label]" (AMS K175244). PARATYPES: **Tasmania**: 1♂, 1♀, same data as holotype (AMS).

Diagnosis. Recognized by the strong inflexion of R_{2+3} around the stigma, heavily sclerotized and broad male cerci, and short, narrow posterior and bilobed anterior hypandrial processes. Females can also be partially identified on the basis of a broad, yellow pleural band extending to the katepisternum.

Description. Wing length 3–3.3 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Antenna with length of scape slightly less than height of eye; postpedicel length less than height of head; three-segmented stylus longer than postpedicel; segment 8 elongate, 4× as long as wide. Palpus brown, slender, one-sixth length of labrum.

Thorax. Scutum and postnotum dark brown; upper margin of pleura brown, remaining pale brown; postpronotal lobe pale; long, broad yellow pleural band extending to katepisternum; scutum lacking vitta of pruinescence.

Wing as in *C. attenuatus*.

Legs. Fore and mid coxae and ventral margin of femora pale yellow, remaining leg segments brown, darker towards tip. First tarsomere greater than half length of fore tibia.

Mid femur slender with pv row of long, dark setae; proximal half with av row of dark setae, increasing in length basally, biserial at base. Mid tibia very slightly swollen at mid-length, with 4 stout av; pv surface with row of slender setae, longer than width of tibia; ventroapically with row of short erect setae on apical fourth; 1 ad seta on proximal half. First tarsomere ⅘ length of remaining 4 tarsomeres, with 4 erect pv setae.

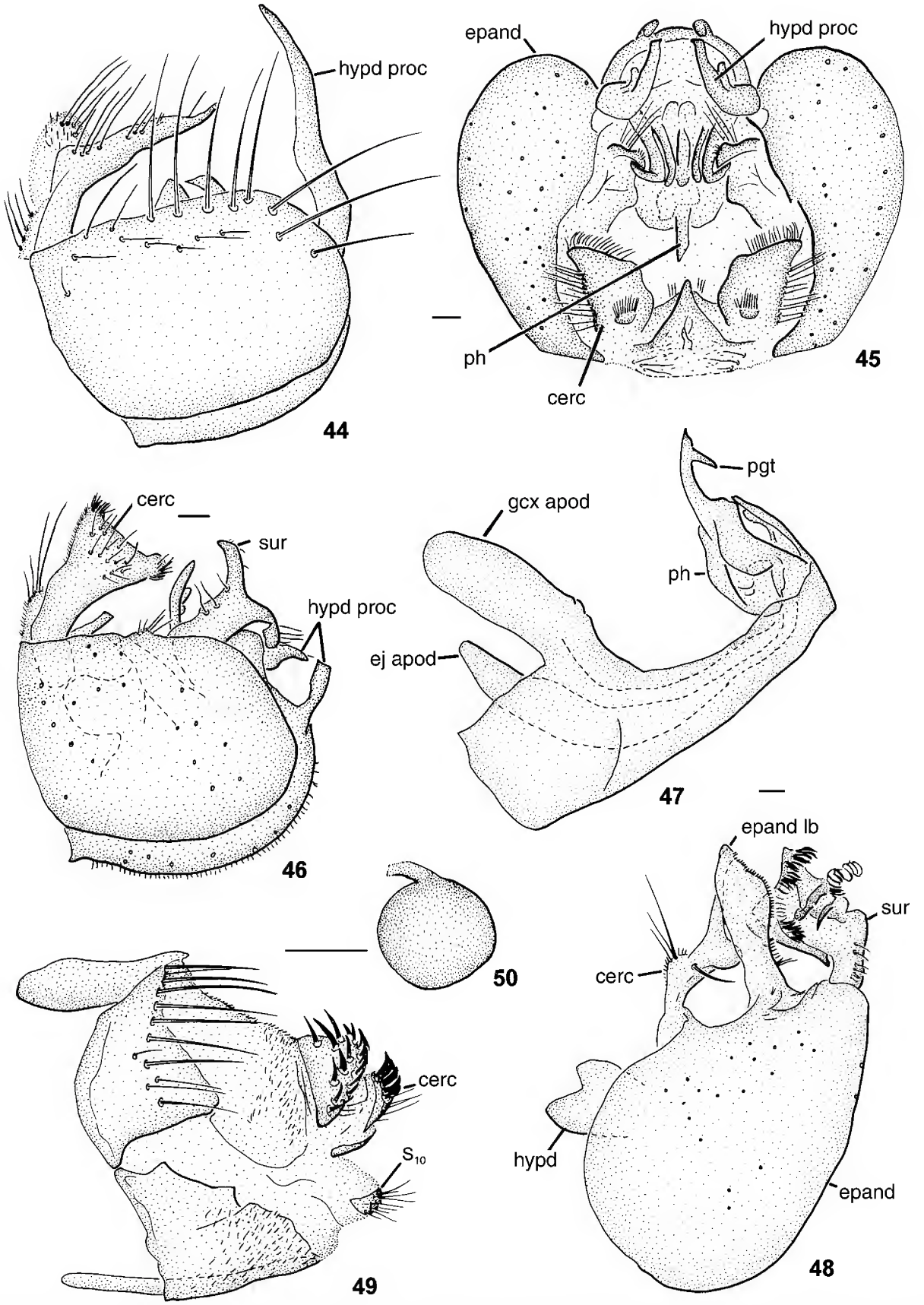
Hind femur straight with 1 preapical dorsal and 1 ad seta; ventral surface with av row of fine setae, shorter than width of femur. Hind tibia with 2 erect dorsal setae on apical half; 4 erect ad setae. Hind tarsomeres slightly longer than tibia.

Abdomen pale brown, concolorous with thorax, sclerites thinly sclerotized; T8 bow-tie shaped, with very short ventral process.

Terminalia (Figs. 45, 46). Hypandrium with pair of short, slender posterior processes; 1 pair of short anterior, bilobed, hooked, articulated processes arched posteriorly near surstyli; postgonites arched anteriorly, flanking pair of phallic processes; stout, blade-like, median phallic process arched anteriorly, distant from postgonites and posterior phallic processes. Epandrial lamella greatly inflated laterally, round; fused ventrally to lateral wall of hypandrium. Surstylus hammer-shaped, shorter than cercus. Subepandrial plate subrectangular, heavily sclerotized; more than half length of cercus. Cercus heavily sclerotized, long and broad in posterior view; apex expanded with fringe of subapical setae; strong setae clustered along anterior and posterior margins.

Female. Similar to male and female of *C. attenuatus* except as follows: Terminalia (based on undissected specimen): T10 bearing stout setae; cercus bearing similar modified setae.

Distribution. This species is restricted to Tasmania (Fig. 100).



Figs. 44–50. Terminalia of *Ceratomerus*. 44, *C. bickeli*, male, lateral view. 45–46, *C. bulbosus*: 45, male, dorsal view; 46, male, lateral view. 47–50, *C. globosus*: 47, hypandrium and phallus, lateral view; 48, male, lateral view; 49, female, lateral view; 50, spermatheca. Scale bars = 0.1 mm. Abbreviations: *cerc*, cercus; *gcx apod*, gonocoxal apodeme; *ej apod*, ejaculatory apodeme; *epand*, epandrium; *epand lb*, epandrial lobe; *hypd*, hypandrium; *hypd proc*, hypandrial process; *pgt*, postgonite; *ph*, phallus; *S*, sternite; *sur*, surstylus.

Etymology. The specific name is from the Latin *bulbosus* (swollen), referring to the greatly swollen or inflated male hypopygium.

Ceratomerus globosus n.sp.

Figs. 39, 40, 42, 47–52, 57

Type material. HOLOTYPE ♂, "AUST[ralia]: NSW[New South Wales]: Kosciusko/ NP, nr. Swamp Plain/ 28.ix.1994, 500 m/ B.J. Sinclair/ ex. Bogong Ck."; "HOLOTYPE/ *Ceratomerus*/ *globosus*/ Sinclair [red label]" AMS K175245. PARATYPES: **New South Wales**: 3♂♂, 3♀♀, same data as holotype (AMS, CNC); 1♂, 1♀, Barrington Tops NP, upper Gloucester R. + Falls, 1200 m, 20–21.xii.1993. BJS (CNC); 1♀, Barrington Tops NP, Williams R., subtrop. rainfor., 480 m, 19.xii.1993, BJS; 1♀, Blue Mtns NP, Valley of the Waters, Vera Falls, 23.x.1994, BJS; 1♂, 1♀, Blue Mtns NP, Wentworth Falls, Jamison Ck, 10.xi.1993, 23.x.1994, BJS (ZFMK); 1♂, Jonolan, 12.x.1950 (UQIC); 2♂♂, 1♀, Kosciusko NP, Leatherbarrel Ck, 1000 m, 28.xi.1994, BJS, DJB (AMS). **Victoria**: 5♂♂, 5♀♀, Burrowa-Pine Mtn NP, Bluff Ck Falls, 400 m, riverine for., y.pans, 29.xi.1994, DJB (ANIC, AMS); 1♀, Delgate R. & Goonmirk Rd, 960 m, 16.i.1991, DJB; 2♀♀, Otway Ra., SE Beech For., Beauchamp Falls, y.pans, mixed forest, 4–5.xii.1994, DJB; 1♀, Otway Ra., Beauchamp Falls, *Nothofagus*, 3.xii.1994, BJS (AMS); 3♂♂, 1♀, 45 km N Orbost, Bonang Hwy, Martins Ck, rainfor., 200 m, 6.xii.1994, BJS (CNC); 1♂, 29.5 km N Warburton, Acheron Way, rainfor., Acheron R., 1.xii.1994, BJS (ZFMK).

Additional material. New South Wales: 1♀, Styx R. SF, E Jeogla, Wattle Flat, wet scler. for., pans, 1000 m, 7.xii.1992, DJB (AMS). This specimen is possibly conspecific because the ratio of the length of the style to postpedicel is similar, but an associated male specimen is required for confirmation.

Diagnosis. Recognized by the style shorter than the postpedicel, slight inflexion of R_{2+3} around the stigma, dark brown pleura, tufts of stout setae on the lateral margin of male sternites 3–4 and tergite 6, encapsulated male terminalia, and scape 1.25 times longer than height of head.

Description. Wing length 3.5–4 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Face pale brown. Antenna with length of scape 1.25× height of eye (Fig. 57); postpedicel apical half 1.25× length of base; three-segmented stylus one-third length of postpedicel; segment 8 short, slightly longer than width. Palpus yellow, slender, one-fifth length of labrum.

Thorax. Scutum, postnotum and pleura dark brown; postpronotal lobe pale; pale streak extending ventrally along proepisternum.

Wing (Fig. 51) as in *C. attenuatus*.

Legs. Base of femora, especially inner margin yellow, becoming dark brown towards tip. Fore femur slightly swollen, lacking ventral setae. First tarsomere greater than half length of fore tibia, with large notch on apical third; base of notch with twisted spur-like seta (Fig. 40).

Mid femur more strongly swollen than fore femur, apical fourth strongly constricted; mid-length bearing pv row of 3 setae, longer than width of femur; apical half of swollen portion with 4 transverse rows of stout setae; base with long erect pv seta (Fig. 39). Mid tibia about half as long as femur, somewhat flattened and twisted, with subapical av notch; lateral margins with av and pv rows of setae, latter row increasing in length apically; lacking erect ad setae. First tarsomere longer than remaining 4 tarsomeres, with many erect pv setae.

Hind femur straight with ventral surface bearing av row of short, dark setae. Hind tibia with 2 erect dorsal setae on apical half; ad margin with row of 3 long, erect setae. Hind tarsomeres slightly longer than tibia.

Abdomen. S3–4 and T6 with dense cluster of short, stout, lateral setae; T8 broad, subrectangular, about half as long as sternite.

Terminalia (Figs. 47, 48). Hypandrium laterally flattened, enclosed within epandrial lamellae; apex produced into slender posterior flap-like process; gonocoxal apodemes well developed; postgonites upright, gently arched posteriorly with subapical hooked process; phallus with pair of articulated processes, flanked by postgonites. Epandrial lamella oval forming distinct capsule fused ventrally to hypandrium; bearing subapical epandrial lobe, apically tapered, with dense mat of microtrichia. Surstylus complex, twisted, strongly bent, bearing whip-like setae; anterior margin with fringe of stout setae. Subepandrial plate narrow; lacking processes from hypoproct. Apical half of cercus well sclerotized, very narrow with apex bearing many stout setae; long stout seta on lateral margin of basal half.

Female. Similar to male and female of *C. attenuatus* except as follows: apical half of palpus brown. Wing similar to male (Fig. 52). S7 lacking transverse weakening. Terminalia (Fig. 49): cercus bearing row of spine-like setae, with long slender marginal setae. Spermatheca receptacle spherical, with short, pigmented neck (Fig. 50).

Distribution. This species is recorded from isolated communities at least as far north as Barrington Tops (NSW) south to the Otway Ranges of Victoria (Fig. 42).

Biology. This species appears to prefer cool temperate rainforest regions and is more rarely collected along gallery rainforests.

Etymology. The specific name is from the Latin *globosus* (round as a ball), referring to the rounded, encapsulated hypopygium.

Ceratomerus inflexus Hardy

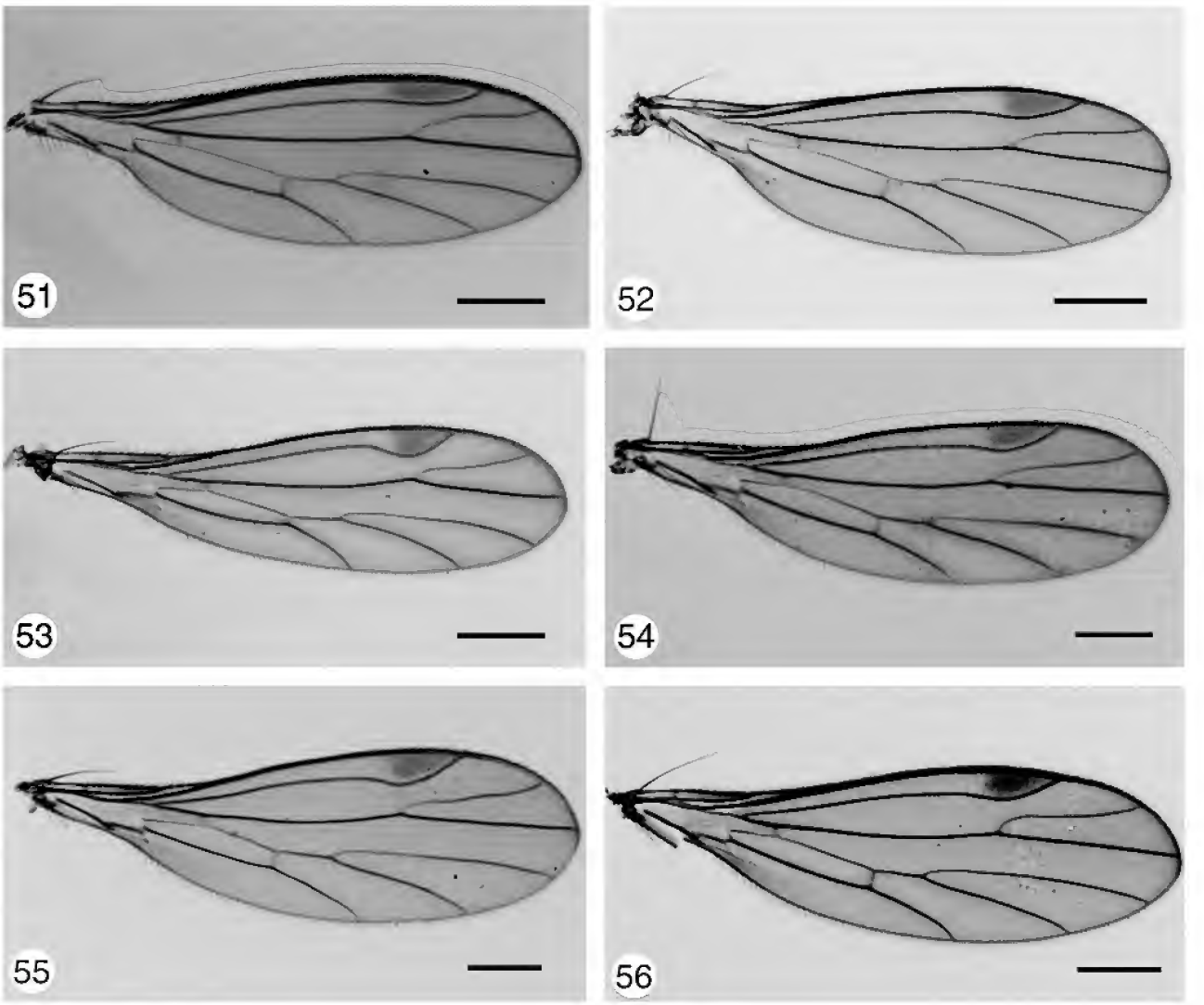
Figs. 53, 63, 71

Ceratomerus inflexus Hardy, 1930: 247.

Type material. NEOTYPE (here designated) ♂, "TAS[mania, Australia]: Sandy Bay [Hobart]/ creek, U[niversity of].Tas. campus/ 18–21-1-1993; pans/ wet scler; D. Bickel"; "NEOTYPE/ Ceratomerus/ inflexus Hardy/ des. B.J. Sinclair 2000 [red label]" AMS K175253.

As discussed in "Materials and methods", all Hardy type series have been lost, and this species, *C. inflexus*, was not mentioned in the list of damaged Hardy types by Daniels (1978). But it was possible to associate this species on the basis of wing venation. In addition, the original type material was collected from Mount Nelson (Hardy, 1930), which is a suburb near Sandy Bay (Hobart) and the University campus where the Neotype was collected. The description by Hardy (1930) of the hypopygium as "rather small" is considered incorrect and was likely confused with *C. ordinatus*. Given the inaccuracies of the original description which may lead to future misidentifications, the designation of a neotype was deemed necessary.

Additional material. Australian Capital Territory: 1♂, 2♀♀, Blundells Ck, 35°22'S 148°50'E, vi, viii.1987 (ANIC). **Tasmania**: 1♀, same data as neotype (AMS). **Victoria**: 2♂♂, 1♀, Alexandra, 27.v.1953 (ANIC, MVM); 1♂, Burrowa-Pine Mtn NP, Bluff Ck, picnic area, 400 m, rainfor., y.pans, 29.xi.1994 (AMS).



Figs. 51–56. Wings of *Ceratomerus*. 51–52, *C. globosus*: 51, male; 52, female. 53, *C. inflexus*, male. 54–55, *C. malleolus*: 54, male; 55, female. 56, *C. oreas*, male. Scale bars = 0.5 mm.

Diagnosis. Recognized by the strong inflexion of R_{2+3} around the stigma, inflated male terminalia, stout male cerci, and short, broad posterior and truncate anterior hypandrial processes.

Description. Wing length 3–3.4 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Postocular bristles short, erect shorter than one-third of eye. Antenna with length of scape slightly less than height of eye, with 3 dorsal setae; postpedicel length less than height of head; three-segmented stylus longer than postpedicel; segment 8 elongate, 4× as long as wide. Palpus brown, slender, one-sixth length of labrum.

Thorax. Scutum and postnotum dark brown; upper margin of pleura brown, remaining pale brown; postpronotal lobe pale.

Wing (Fig. 53). R_{2+3} running parallel and close to costa, strongly deflected around stigma.

Legs. Fore and mid coxae and ventral margin of femora pale yellow, remaining leg segments brown, darker towards tip. First tarsomere greater than half length of fore.

Mid femur slender with pv row of long, dark setae; base with long erect pv seta; proximal half with av row of dark setae, increasing in length basally, biserial at base. Mid tibia slightly swollen at mid-length, bearing 2–3 stout av setae; pv surface with row of slender setae, longer than width of tibia; av surface with row of setae, decreasing in length apically; apical 4–5 av setae, shorter than width of tibia, held erect, perpendicular to tibia; 2 ad setae on proximal half. First tarsomere ⅗ length of remaining 4 tarsomeres, with 4 erect pv setae.

Hind femur straight with 1 preapical dorsal and 1 ad seta; ventral surface with av row of fine setae, shorter than width of femur. Hind tibia with 2 erect dorsal setae on apical half; 4 erect ad setae. Hind tarsomeres slightly longer than tibia.

Abdomen pale brown, concolorous with thorax, sclerites thinly sclerotized; T8 bow-tie shaped, with short ventral process.

Terminalia (Fig. 63). Hypandrium with pair of short posterior processes; 1 pair of short, anterior, hooked articulated processes arched posteriorly near surstyli, with truncate apex; postgonites arched anteriorly, flanking pair of phallic processes; stout, blade-like, median phallic process arched anteriorly, distant from postgonites and posterior phallic processes. Epandrial lamella greatly inflated laterally, spherical; fused ventrally to lateral wall of hypandrium. Surstylus finger-shaped, shorter than cercus.

Subepandrial plate trapezoidal, heavily sclerotized; more than half length of cercus. Cercus heavily sclerotized, long and broad in posterior view; apex expanded with fringe of subapical setae; strong setae clustered along anterior and posterior margin.

Female. Similar to male and female of *C. attenuatus* except as follows: Terminalia (based on undissected specimen): T10 bearing stout setae; cercus bearing similar modified setae.

Distribution. This species is known from Tasmania, Victoria and the Australian Capital Territory (Fig. 71).

Remarks. The mainland population differs somewhat from the neotype in having more pronounced setae on the inner margin of the surstylus.

Ceratomerus malleolus n.sp.

Figs. 41, 54, 55, 58, 64–68, 71

Type material. HOLOTYPE ♂, "VIC[toria, Australia]: Acheron Creek; 29 km/ from Warburton; pans/ rainforest/creek; 400 m/ 1–3.xii.1994; D. Bickel"; "HOLOTYPE/ *Ceratomerus*/ *malleolus*/ Sinclair [red label]" AMS K175246. PARATYPES: **New South Wales**: 1♂, Kosciusko NP, Pipers Ck, Guthega Rd, 1320 m, subalpine, 1.i.1991, DJB (AMS). **Victoria**: 1♀, same data as holotype, BJS (ZFMK); 13♂♂, 6♀♀, same data as holotype (AMS, CNC, ZFMK); 1♂, Otway NP, Blanket Bay; rocky ck above falls, 10 m, 4–5.xii.1994, y.pans, DJB (AMS).

Diagnosis. Recognized by the slight inflexion of R_{2+3} around the stigma, heavily sclerotized male tergites 4–6 and anvil-shaped male cercus. This species can be distinguished from its sister species, *C. macalpinei*, by the narrow setose lobe beneath the cercus. Females can be partially identified by the brown pleura and long style.

Description. Wing length 3–3.5 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Postocellar bristles one-third length of ocellar bristles. Antenna with length of scape slightly less than height of eye (Fig. 58); postpedicel length less than height of head; three-segmented stylus longer than postpedicel; segment 8 elongate, 4× as long as wide. Palpus one-fifth length of labrum.

Thorax. Pale streak occasionally extending ventrally along proepisternum.

Wing (Fig. 54) as in *C. attenuatus*.

Legs. Fore and mid coxae pale and ventral margin of femora yellowish-brown, remaining leg segments brown, darker towards tip. Fore femur slightly swollen, with av row of fine setae, decreasing in length apically; basal setae longer than width of femur. First tarsomere greater than half length of fore tibia.

Mid femur with pv row of short, dark setae; base with long erect pv seta; basal half with av brush of short dark setae, increasing in length medially (Fig. 41). Mid tibia not swollen at mid-length, with av row of short setae; pv surface with row of slender setae, longer than width of tibia; ventroapically with row of short erect setae on apical sixth; 1 ad seta on proximal half. First tarsomere subequal in length to remaining 4 tarsomeres, with many erect pv setae.

Hind femur straight with 1 preapical dorsal and 1 av seta; ventral surface with av row of short, fine setulae. Hind tibia with 2 erect ad setae on apical half; dorsal margin with row of 4 long, erect setae. Hind tarsomeres slightly longer than tibia.

Abdomen pale brown, concolorous with thorax, sclerites of segment 1–3 weakly sclerotized; T4–6 heavily sclerotized, lateral margin extending ventrally, most pronounced in T4, where stout, rounded ridge formed (Fig. 68); S7 produced laterally, overlapping T7; T8 bow-tie shaped, lacking ventral process.

Terminalia (Figs. 66, 67). Hypandrium with pair of short, slender posterior processes; 1 pair of short anterior, hooked, articulated processes arched posteriorly near surstyli; postgonites arched anteriorly, flanking pair of phallic processes; stout, blade-like, median phallic process arched anteriorly, with hooked apex. Epandrial lamella greatly inflated laterally, spherical; fused ventrally to lateral wall of hypandrium. Surstylus curved, finger-like, shorter than cercus. Subepandrial plate subrectangular, heavily sclerotized; more than half length of cercus. Hypoproct with large, lateral process, curving out from beneath cercus; apex round. Cercus heavily sclerotized, with narrow neck and laterally expanded, hammer-shaped apex; clothed in fine setulae, lacking long setae; base of cercus with slender setose lobe.

Female. Similar to male and female of *C. attenuatus* except as follows: wing similar to male, although often R_{2+3} more strongly deflected below stigma (Fig. 55). S7 with transverse weakening, providing flexibility. Terminalia (Fig. 64): anterior margin of T8 with flattened, internal, median plate, strongly arched ventrally. S8 subdivided into small trapezoidal sclerite and small, oval dome-shaped sclerite; posterior margin invaginated, forming broad internal plate. T10 bearing stout setae along posterior margin. Cercus bearing similar modified setae. Spermathecal receptacle oval, flattened, with distinct wide neck (Fig. 65).

Distribution. This species is known from Victoria and New South Wales (Fig. 71), in subalpine to coastal habitats.

Etymology. The specific name is from the Latin *malleolus* (hammer), referring to the shape of the male cercus.

Ceratomerus macalpinei n.sp.

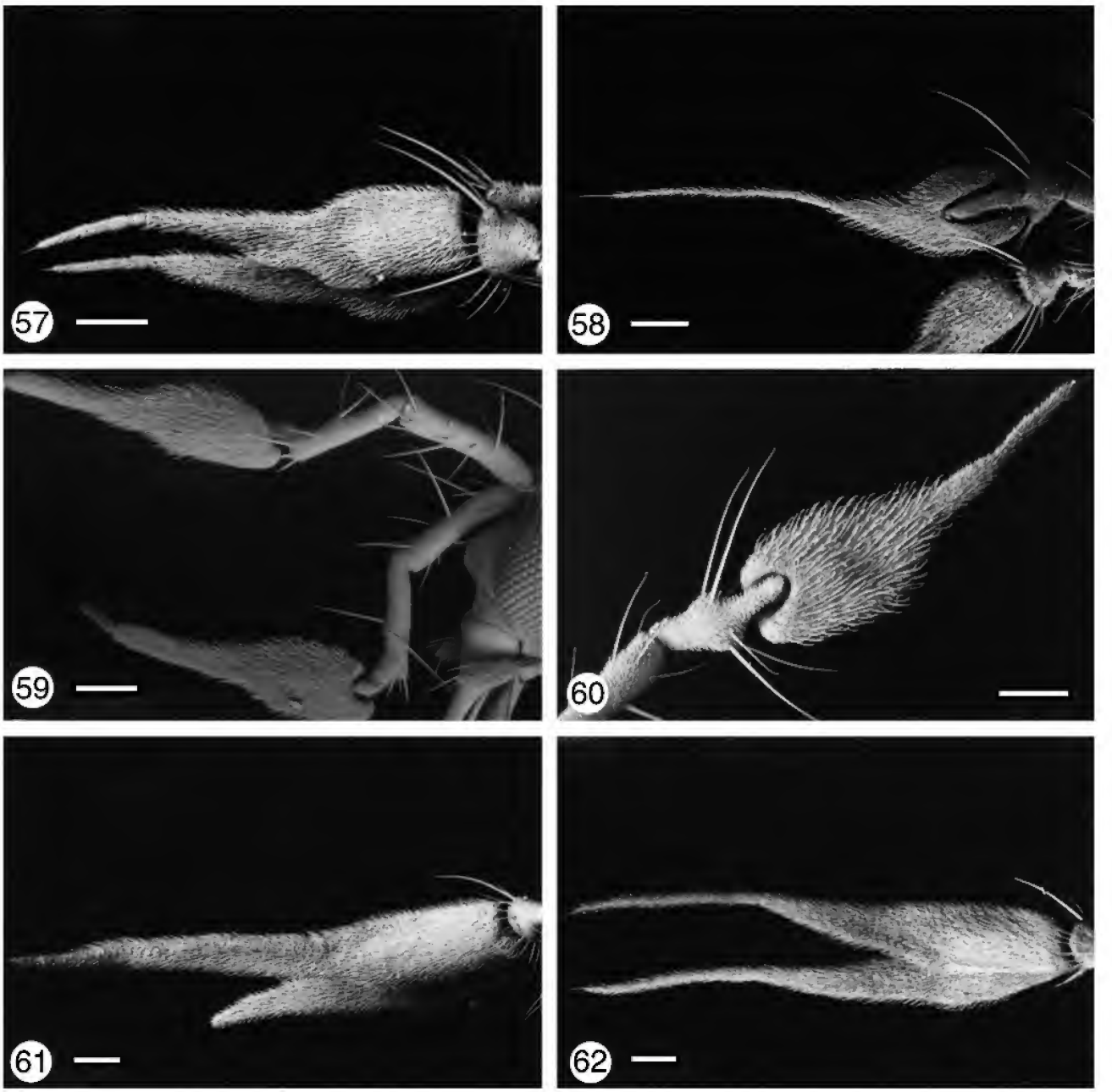
Figs. 69, 71

Type material. HOLOTYPE ♂, "[Aust: NSW]/ Blue Mts. NP, Mt. Wilson, / Waterfall CK, / 12–13.Dec.1998/ YPans, B.J. Sinclair"; "HOLOTYPE/ *Ceratomerus*/ *macalpinei*/ Sinclair [red label]" AMS K175247. PARATYPES: **New South Wales**: 1♂, 3♀♀, same data as holotype; 1♂, same locality, 21.xi.1993 (CNC, ZFMK); 1♂, 1♀, Katoomba, 26.x., 18.xi.1955, G.H. Hardy; 1♂, 1♀, Blue Mtns NP, Mt. Wilson, 19.xii.1986, DKM, B.J. Day, R. de Keyzer; 2♂♂, Morton NP, nr Milton, Cooyoyo Ck, 500 m, 35°17'S 150°11'E, 6.xi.1997, A. Leask (AMS); 1♀, Mt. Wilson, 19.xi.1921, A. Tonnoir (ANIC).

Diagnosis. Recognized by the slight inflexion of R_{2+3} around the stigma, broad, yellow pleural band broad extending to katepisternum, heavily sclerotized male tergites 4–6 and anvil-shaped male cercus. This species can be distinguished from *C. malleolus* by the narrow lobe beneath the cercus, which is roundly expanded apically and tapered posterior tip of the cercus.

Description. Wing length 3.3–3.5 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Postocellar bristles short, one-third length of ocellar bristles. Antenna with length of scape slightly less than height of eye; postpedicel length less than height of head; three-segmented stylus longer than postpedicel;



Figs. 57–62. Scanning electron micrographs of antennae of *Ceratomerus*. 57, *C. globosus*, male, outer view. 58, *C. malleolus*, male, inner view. 59, *C. maculatus*, male. 60, *C. ordinatus*, female, inner view. 61–62, *C. albistylus*: 61, male, outer view; 62, female, outer view. Scale bars = 0.1 mm.

segment 8 elongate, 4× as long as wide. Palpus one-fifth length of labrum.

Thorax. Pale streak extending ventrally from proepisternum across pleura.

Wing as in *C. attenuatus*.

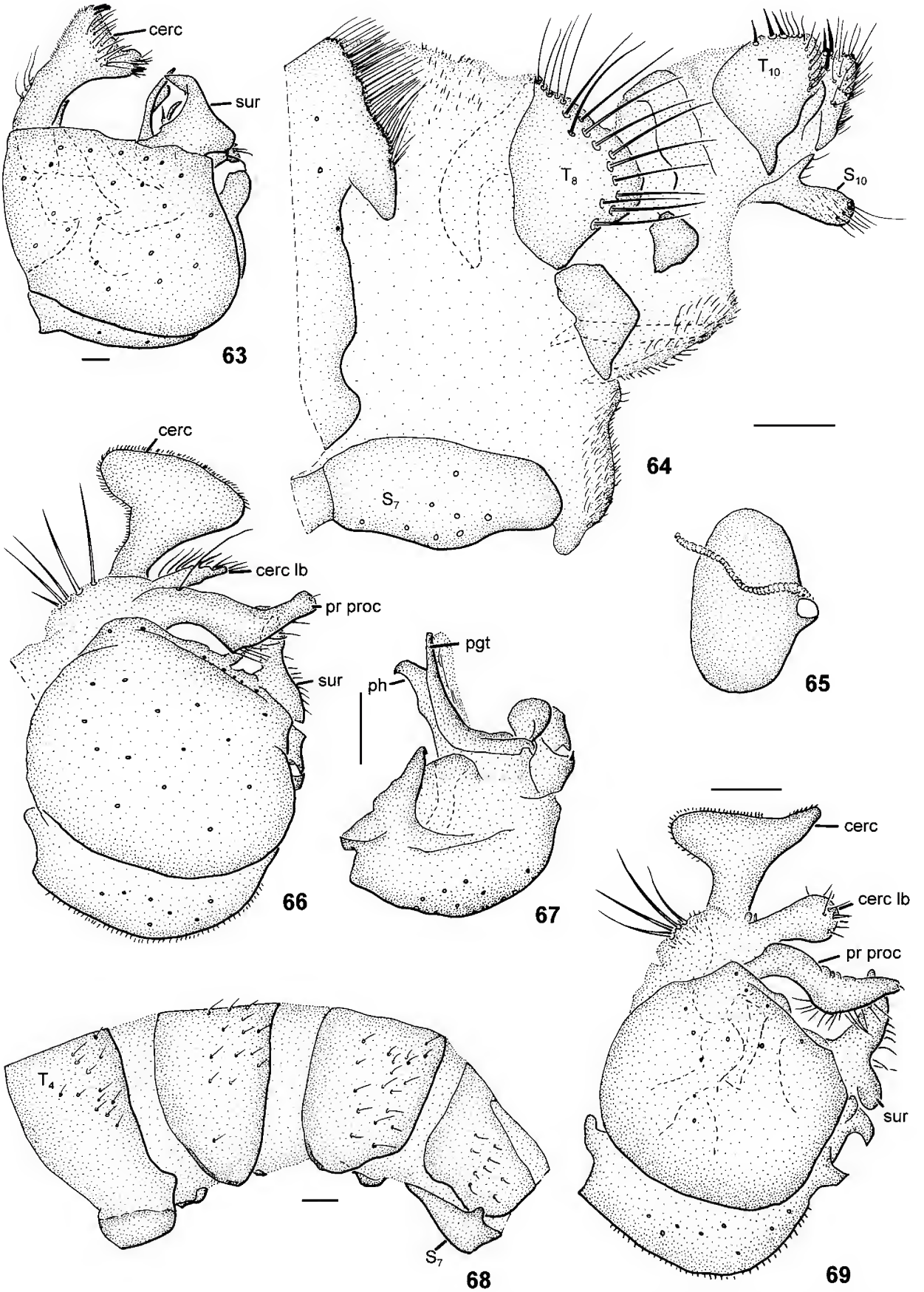
Legs. Fore and mid coxae and ventral margin of femora yellow, remaining leg segments brown, darker towards tip. Fore femur slightly swollen, with av row of fine setae, decreasing in length apically; basal setae longer than width of femur. First tarsomere greater than half length of fore tibia.

Mid femur more strongly swollen than fore femur, with pv row of short, dark setae; base with long erect pv seta; basal half with av brush of short dark setae, increasing in length medially. Mid tibia with pv row of slender setae, longer than width of tibia; ventroapically with row of short erect setae on apical sixth; 1 ad seta near mid-length.

Hind femur straight with 1 preapical dorsal and 1 av seta; ventral surface with av row of short, fine setulae. Hind tibia with 2 erect ad setae on apical half; dorsal margin with row of 3 long, erect setae. Hind tarsomeres slightly longer than tibia.

Abdomen brown, concolorous with thorax, sclerites of segment 1–3 more thinly sclerotized than remaining segments; T4–6 heavily sclerotized, lateral margin extending ventrally, most pronounced on T4, where stout, rounded ridge formed; S7 produced laterally, overlapping T7; T8 bow-tie shaped, lacking ventral process.

Terminalia (Fig. 69). Hypandrium with pair of short, slender posterior processes; 1 pair of short anterior, hooked, articulated processes arched posteriorly near surstyli; postgonites arched anteriorly, flanking pair of phallic processes; stout, blade-like, median phallic process arched



Figs. 63–69. Terminalia and posterior abdomen of *Ceratomerus*. 63, *C. inflexus*, male, lateral view. 64–68, *C. malleolus*: 64, female, lateral view; 65, spermatheca; 66, male, lateral view; 67, hypandrium and phallus, lateral view; 68, male abdomen, lateral view. 69, *C. macalpinei*, male, lateral view. Scale bars = 0.1 mm, except Fig. 68 where scale bar = 0.05 mm. Abbreviations: *cerc*, cercus; *cerc lb*, cercal lobe; *pgt*, postgonite; *ph*, phallus; *pr proc*, proctiger process; *S*, sternite; *sur*, surstylus; *T*, tergite.

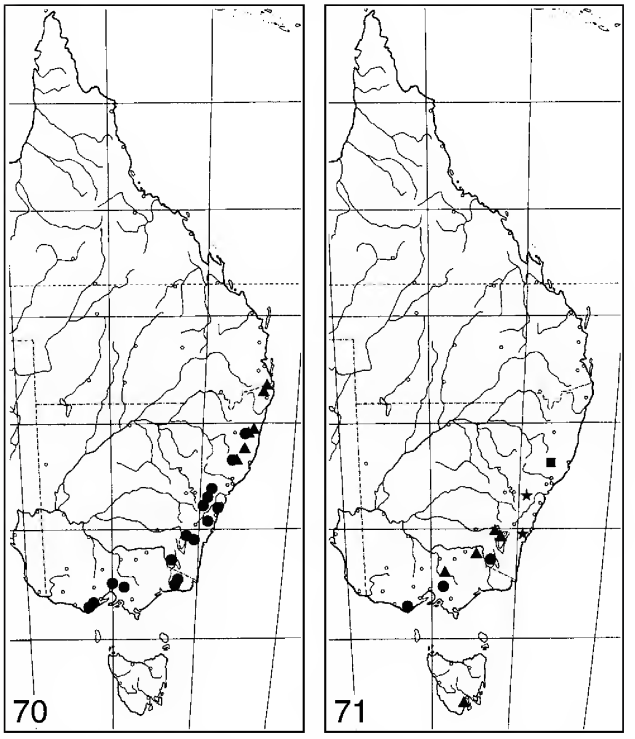
anteriorly. Epandrial lamella greatly inflated laterally, spherical; fused ventrally to lateral wall of hypandrium. Surstylus curved, finger-like, shorter than cercus. Subepandrial plate subrectangular, heavily sclerotized; more than half length of cercus. Hypoproct with large, lateral process, curving out from beneath cercus; apex round. Cercus heavily sclerotized, with narrow neck and laterally expanded, hammer-shaped apex; posterior tip tapered; cercus clothed in fine setulae, lacking long setae; base of cercus with narrow lobe; apex roundly expanded apically.

Female. Similar to male and female of *C. attenuatus* except as follows: S7 with transverse weakening, providing flexibility. Terminalia: anterior margin of T8 with flattened, internal, median plate, slightly arched ventrally. S8 subdivided into small trapezoidal sclerite and small, oval dome-shaped sclerite; posterior margin invaginated, forming broad, sclerotized internal plate. T10 bearing stout setae along posterior margin. Cercus broad laterally bearing similar modified setae. Spermathecal receptacle oval, sides parallel-sided, flattened, with short wide neck.

Distribution. The greatest number of specimens of this species have been collected from the Mt. Wilson region of the Blue Mountains (Fig. 71).

Biology. All specimens at Mt. Wilson were collected along a narrow, cascading stream. This locality is a small remnant rainforest growing in rich basaltic soils, and near the stream is a large grove of tree ferns (*Dicksonia antarctica*), known as the "cathedral of ferns".

Etymology. The specific name honours Dr D.K. McAlpine, who collected several of the type specimens of this species and first introduced the author to the type locality.



Figs. 70–71. Known distribution of species of *Ceratomerus* (eastern Australia). 70, *C. falcatus* ▲, *C. maculatus* ●. 71, *C. inflexus* ▲, *C. malleolus* ●, *C. macalpinei* ★, *C. oreas* ■.

Ceratomerus oreas n.sp.

Figs. 56, 71–75

Type material. HOLOTYPE ♂, "NSW[New South Wales, Australia]: Gloucester Tops/ el.1280; 19-xi–4-xii/ -1988; D.Bickel; mal-/ aise; *Nothofagus* for."; "HOLOTYPE/ *Ceratomerus*/ *oreas*/ Sinclair [red label]" AMS K175248. PARATYPES: **New South Wales**: 7♂♂, 4♀♀, same data as holotype; 1♀, same locality as holotype, 14–19.xi.1988 (AMS); 3♂♂, same locality as holotype, 4–30.xii.1988; 1♂, Barrington Tops NP, Gloucester Tops, Nothofagus, str., 1200 m, 21.xii.1993, BJS (ZFMK); 5♂♂, 1♀, nr Gloucester Tops, 1290 m, *Nothofagus*, 14–19.xi.1988, DJB (AMS, CNC).

Diagnosis. Recognized by the distinct inflexion of R_{2+3} around the stigma, dark pleura, long style and males have distinctive inflated, round epandrial lamellae, and broad, bilobed cercus.

Description. Wing length 3.3–3.6 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Postocellar bristles, short, one-third length of ocellar bristles. Antenna with length of scape one-fourth less than height of eye; postpedicel length less than height of head; three-segmented stylus longer than postpedicel; segment 8 elongate, 4× as long as wide.

Thorax. Pleura light brown.

Wing (Fig. 56). R_{2+3} running parallel and close to costa, strongly deflected around stigma.

Legs. Fore and mid coxae and ventral margin of femora pale yellow, remaining leg segments brown, darker towards tip. Fore femur slightly swollen, with av row of fine setae on basal half. First tarsomere two-thirds length of fore tibia.

Mid femur swollen similar to fore femur, with pv row of short, dark setae; basal half with av brush of short dark setae, increasing in length medially. Mid tibia slender with pv row of slender setae, longer than width of tibia; basal half with av row of short setae; ventroapically with row of short erect setae on apical fourth; 1 ad seta on basal third. First tarsomere ⅘ length of remaining 4 tarsomeres.

Hind femur with av row of fine setae, shorter than width of femur. Hind tibia with 2 erect dorsal setae on apical half; 3 erect ad setae.

Abdomen. S7 with transverse weakening on anterior third; posterior margin of S7 broadly membranous, with well sclerotized posterolateral margin, extending to S8; T8 bow-tie shaped, lacking ventral process.

Terminalia (Figs. 72, 73). Hypandrium with pair of bilobed posterior processes; anterior lobe hooked posteriorly; postgonites erect, with broad base, strongly tapered to slender slightly curved tip; phallic processes absent; stout, blade-like, median phallic process somewhat arched anteriorly. Epandrial lamella greatly inflated laterally, round; fused ventrally to lateral wall of hypandrium. Surstylus with long, slender finger-shaped lobe. Subepandrial plate subrectangular, heavily sclerotized; more than half length of cercus. Cercus heavily sclerotized, short, broad, with bilobed apex; inner margin of anterior lobe with short, stout setae; posterior lobe with dense cluster of long stout setae, longer than width of lobe.

Female. Similar to male and female of *C. attenuatus* except as follows: Terminalia (Fig. 75): T10 bearing single row of spine-like setae along posterior margin. Cercus broad, bearing spine-like setae, with short, slender marginal setae. Spermathecal receptacle oval, flattened, with short wide neck (Fig. 74).

Distribution. This species is restricted to the type locality, an isolated patch of cool temperate rainforest dominated by *Nothofagus* (Fig. 71).

Biology. All specimens were collected from or near cool, shaded mossy streams. The upper plateau of Gloucester Tops supports snow gum and grassland communities, while the gullies and saddles immediately below the plateau support stands of *Nothofagus*. It is in these sheltered wet forests where several species of *Ceratomerus* abide.

Etymology. The specific name is from the Latin *oreas* (mountain-nymph), referring to the high elevation of the type locality.

Ceratomerus ordinatus species-group

This Australian species group of *Ceratomerus* is characterized by a lengthened pedicel (second antennal segment), stigma absent, long postocular bristles overlapping eye, widely spaced ocellar bristles, third dorsocentral bristle shorter than others, and posterior fringe of female tergite 7 lacking. In addition, a number of species have a short, dorsomedian projection from the apex of the fifth tarsomere. Several of the above characters are also present in undescribed species from New Zealand and Ecuador and possibly indicates close phylogenetic relationships among all these taxa.

Species of this group were observed to be quite active runners over rocks in and along the banks of creeks. Upon alighting on a rock, they often immediately run about, in contrast to taxa of other species groups which appear to be much less active and reclusive.

Ceratomerus falcatus n.sp.

Figs. 70, 76, 77, 80, 91, 92

Type material. HOLOTYPE ♂, "AUST[ralia]: QLD [Queensland]: Lamington/ N.P., Green Mtns./ 6.v.1994, Elabana Falls/ B.J. Sinclair/ ex. Canungra Ck."; "HOLOTYPE/ *Ceratomerus*/ *falcatus*/ Sinclair [red label]" AMS K175249. PARATYPES: **New South Wales**: 1♂, Barrington Tops NP, Gloucester Tops, 1200 m, *Nothofagus*, str., 21.xii.1993, BJS (ZFMK); 1♂, Barrington Tops NP, Williams R., subtrop. rainfor., 19–20.xii.1993, DJB (AMS); 38♂♂, 2♀♀, Barrington Tops NP, Williams R., subtrop. rainfor., 480 m, 19.xii.1993, 21.i.1995, BJS (AMS, CNC); 7♂♂, 3♀♀, 23 km WNW Bellangry, Cockerawombeeba Ck, warm temp. rainfor., 730 m, 8.xii.1986, 14–15.i.1988, DJB (AMS); 26♂♂, Border Ranges NP, Brindle Ck, 1000 m, rainfor., 25–26.i.1995, BJS (ANIC, CNC, ZFMK); 2♂♂, Chichester SF, Allyn R., 22.i.1995, BJS; 1♀, Dorrigo NP, 2–15.x.1984, MT, I. Naumann, J. Cardale (ANIC); 5♂♂, 1♀, Dorrigo NP, Rosewood Ck, 23.i.1995, BJS (CNC); 5♂♂, 1♀, Dorrigo NP, Sassafras Ck 700 m, Callicoma Falls, subtrop. rainfor., 1.iv.1995, BJS (ZFMK); 3♂♂, Mt. Hyland NP, Obeloe Ck, 1030 m, 30°10'S 152°27'E, y.pans, warm temp rainfor., 25–27.i.1996, DJB; 1♂, Werrikimbe NP, N. Plateau Beech For., y.pans, 28.xii.1993, DJB; 5♂♂, 9♀♀, Upper Allyn R., nr Eccleston, 4.v.1967, DKM (AMS). Queensland: 10♂♂, 1♀, same data as holotype (AMS, CNC).

Additional material (in alc.). New South Wales: 1♂, 3♀♀, New England NP, Point Lookout, 30°29'S 152°25'E, 12.ii.1984, I.D. Naumann (ANIC).

Diagnosis. Distinguished from other members of this species group by the simple male wings, with straight veins and lacking spots, and the auxiliary crossvein is present in both sexes. Females are generally difficult to separate from *C. maculatus*, but sometimes distinguished by their more lightly infuscate wings and the radial fork is generally proximal to cell dm.

Description. Wing length 2.1–2.3 mm.

Male. *Head* (Fig. 91) dark brown, dull; face pale brown, lacking setae; ocellar triangle with 2 widely spaced, divergent bristles, inserted anterior to lateral ocelli; postocellar bristle long, two-thirds to subequal to length of ocellar bristle; 2 pairs of long vertical bristles; postocular bristles long, overlapping one-third of eye. Antenna with scape two-thirds height of eye, with 3–4 dorsal setae and 1 long ventral seta; pedicel cylindrical, slightly greater than half length of scape; setae confined to apical fringe. Postpedicel covered by long, dense pruinescence, less than 1.5× height of head; basal half rectangular; apical half narrow, nearly parallel-sided, not strongly tapered; three-segmented stylus one-fourth length of postpedicel; segment 8 short, width subequal to length; stylus concolorous with remaining segments. Base of labrum lacking dorsal process; palpus yellowish-brown, slender, one-sixth length of labrum, with several dark setae; prementum with short setae only.

Thorax. Scutum and postnotum dark brown; pleura brown, darker along dorsal margin; postpronotal lobe brown; scutum lacking vitta of pruinescence. Alternating row of short acrostichals to prescutellar depression, subequal in length, directed posteriorly; 4 dc, third dc short and slender; 1 pprn; 1 presut spal; 2 npl, lower weak; 2 psut spal; 1 pal; 4 sctl, outer pair short, slender; additional setulae lacking. Antepronotum lacking setulae.

Wing (Fig. 80) infuscate, stigma lacking; single short costal seta; costal margin with unmodified setulae; posterior margin lacking incision; posterior setal margin complete, unmodified. R_{2+3} gradually arched to C, not deflected; radial fork bell-shaped; medial fork distal to radial fork; cell dm rectangular, slender; auxiliary crossvein between R_{2+3} and R_4 (occasionally absent on one wing). Halter with pale brown knob.

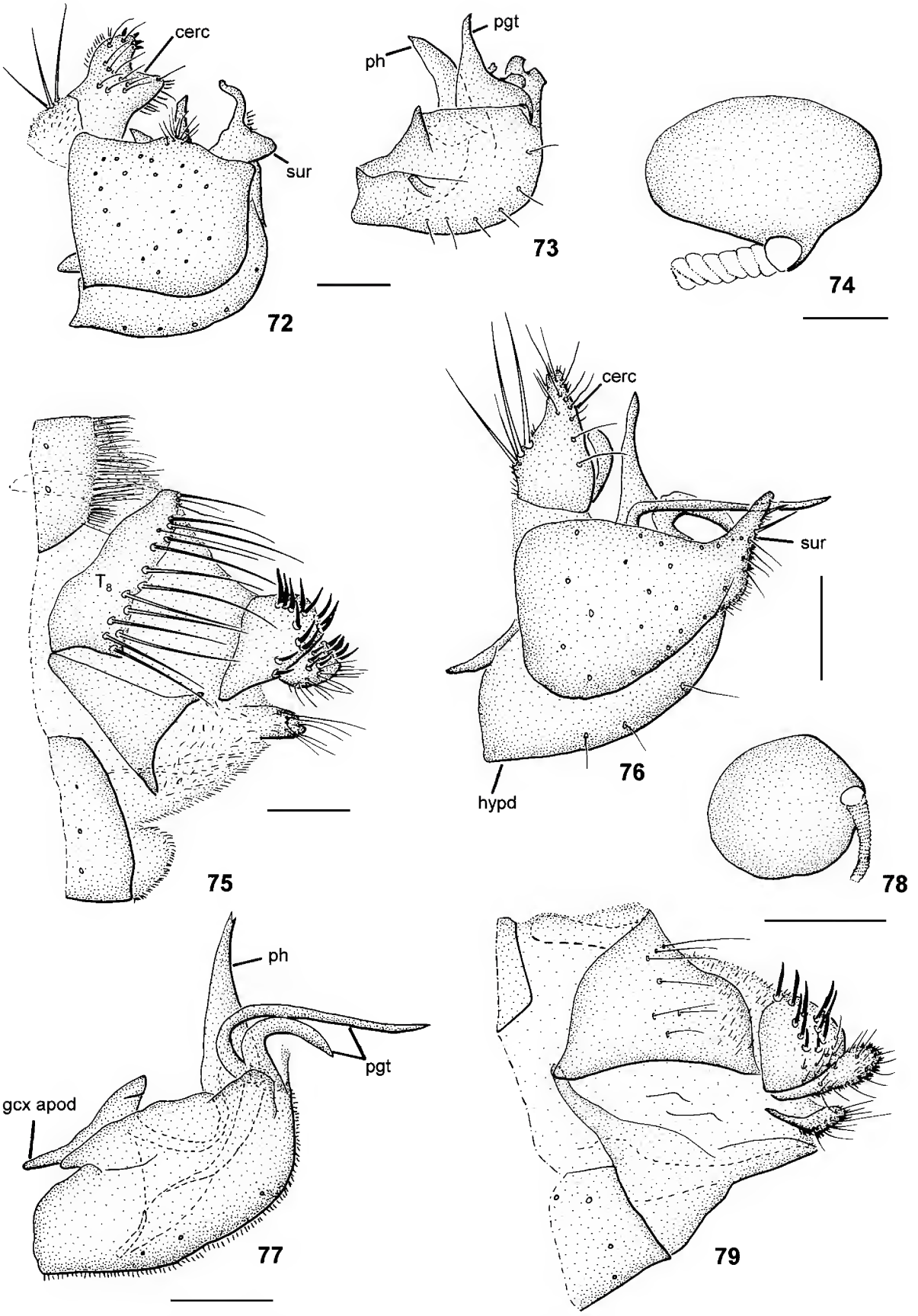
Legs. Coxae yellowish brown, remaining leg segments brown, darker towards tip. Fore coxa about twice length of mid coxa, with long dark anterior setae. Fore trochanter lacking modified setae. Fore femora slightly swollen, with av row of dark setulae; pv region with 2 basal setulae. Fore tibia slightly shorter than femur; apex with anteroapical comb, not dilated. First tarsomere greater than half length of fore tibia; tarsomeres 1–3 slender, tarsomeres 4 and 5 dorsoventrally flattened.

Mid coxa lacking modified seta. Mid femur slender with unmodified setae. Mid tibia subequal in length to femur; lacking erect setae. First tarsomere equal in length to remaining 4 tarsomeres; tarsomere 5 dorsoventrally flattened.

Hind coxa with unmodified setae. Hind femur straight with 1 preapical dorsal seta. Hind tibia straight, shorter than femur, apex dilated, bearing posteroapical comb; pv surface lacking setae. Hind tarsomeres longer than tibia; first tarsomere with 1 short, erect ventral seta near base; tarsomere 5 dorsoventrally flattened.

Abdomen pale brown, sclerites thinly sclerotized, posteromarginal setae short, longest on T6; sclerites lacking ridges and modified setae; central region of T7 membranous; S7 slightly longer than preceding sclerite, lacking posterolateral extension; T8 slender, with broad rectangular posterior membranous zone.

Terminalia (Figs. 76, 77, 92). Hypandrium with short posterior flap-like process; 2 pairs of sickle-shaped, articulated postgonites flanking phallus, outer pair shorter, strongly recurved, inner pair long, slender. Phallus comprises single, straight, pointed median process. Apical corner of epandrial lamella narrow; posterior margin with long setae along inner posterior margin. Surstylus weakly



Figs. 72–79. Terminalia of *Ceratomerus*. 72–75, *C. oreas*: 72, male, lateral view; 73, hypandrium and phallus; 74, spermatheca; 75, female, lateral view. 76–77, *C. falcatus*: 76, male, lateral view; 77, hypandrium and phallus, lateral view. 78–79, *C. hibernus*: 78, spermatheca; 79, female, lateral view. Scale bars = 0.1 mm, except Figs. 76–77 where scale bar = 0.05 mm. Abbreviations: *cerc*, cercus; *gcx apod*, gonocoxal apodeme; *hypd*, hypandrium; *pgt*, postgonite; *ph*, phallus; *sur*, surstylus; *T*, tergite.

developed, with only partial subapical weakening on epandrium. Cercus thinly sclerotized, short, apex blunt, expanded laterally around anus.

Female. Similar to male except as follows: pedicel slightly greater than half length of scape; palpus brown; setae and modifications of legs lacking; pleura brown. Apical segments retracted into segment 7; apical margin of segment 7 not folded inwards; T7 lacking posterior fringe of setae; lateral margin of S7 straight. Terminalia: central region of T8 with deep U-shaped weakly sclerotized zone; fringe of long setae along lateral ridge; anterior margin with broad, flattened, median process, extending beneath T7 when segment retracted; S8 the posterior margin invaginated, forming internal flooring. T10 split medially into pair of rectangular sclerites; anterior margin with stout, straight, spine-like setae; cercus with terminal cluster of 4–5 spine-like setae, similar to T10. Spermathecal receptacle spherical, with short neck where duct attached.

Distribution. This species is distributed from the Border Ranges at the New South Wales and Queensland border, south to Barrington Tops at elevations generally above 400 m (Fig. 70).

Etymology. The specific name is from the Latin *falcatus* (sickle-shaped), referring to the shape of the male postgonites.

Ceratomerus hibernus n.sp.

Figs. 78, 79, 81, 100

Type material. HOLOTYPE ♀, "AUST[ralia]: TAS[mania]: Pelion Hut/ 3 km S Mt. Oakleigh/ 41°50'S 146°03'E, 860 m/ June 1990; I.D. Naumann"; "HOLOTYPE/ *Ceratomerus*/ *hibernus*/ Sinclair [red label]" (ANIC). PARATYPES: **Tasmania:** 6♀♀, same data as holotype (ANIC); 6♀♀, 28 km SSW Mole Ck, 570 m, MAP 8114 355.752, 15.x.1985, L. Hill (AMS, ZFMK).

Diagnosis. Distinguished from other species in this group by the short postocellar setae, long pedicel (three-fifths length of scape) and median fork separated from radial fork by more than the length of crossvein dm-cu.

Description. Wing length 3–3.3 mm, similar to *C. falcatus* except as follows:

Female. *Head* dark brown; postocellar bristle slender, less than half length of ocellar bristle; 3 pairs of long vertical bristles, third pair distant from others; postocular bristles long, overlapping at least one-third of eye. Antenna with scape equal to height of eye, with 2–3 long, dorsal setae and 1 long ventral seta; pedicel with short basal section, three-fifths length of scape, with posterior fringe of long setae; postpedicel apical half strongly tapered, extending parallel-sided to short, stout, three-segmented stylus, subequal to one-third length of postpedicel. Palpus light brown, slender, one-fifth length of labrum.

Thorax. Mesonotum, pleura and postnotum brown; 1 slender, short pal. Antepronotum with 2 short setulae.

Wing (Fig. 81). Medial fork proximal to radial fork by more than length of crossvein dm-cu. Halter with dark knob.

Legs. Coxae and basal half of femora yellowish-brown, remaining leg segments brown, gradually darkening towards tip. Fore coxa lacking modified setae. Fore femur slightly swollen, lacking modified ventral setae. Fore tibia nearly equal in length to femur; apex with undilated anteroapical comb. First tarsomere slightly longer than half length of fore tibia; distal 4 tarsomeres slender, longer than first tarsomere.

Mid tibia slightly shorter than femur with dorsal and ventral apical seta. First tarsomere shorter than remaining 4 tarsomeres.

Hind tibia with 3–4 erect ad setae on apical half; lacking dorsal setae.

Abdomen as in female *C. falcatus*.

Terminalia (Fig. 79). Anterior margin of T10 bearing biserial row of stout, straight spine-like setae; cercus with slender setae, lacking spine-like setae. Spermathecal receptacle spherical, with very short neck where duct attached (Fig. 78).

Male. Unknown.

Distribution. This species is known only from the northwestern highlands of Tasmania (Fig. 100) and is possibly restricted to the cooler months (June, October).

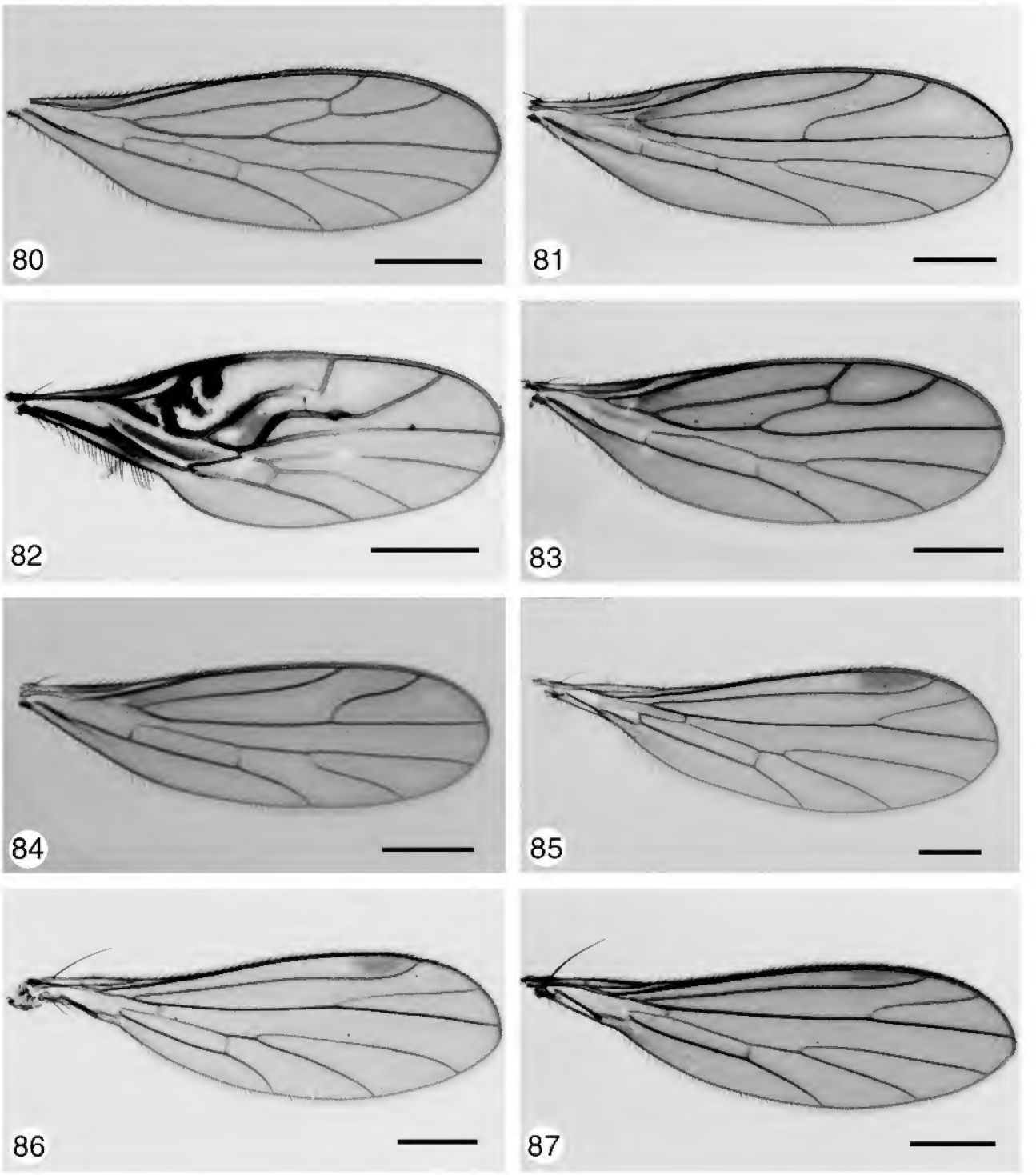
Etymology. The specific name is from the Latin *hibernus* (of winter), referring to the probable seasonality of this species.

Remarks. It is normally not recommended to describe a new species on the basis of female specimens alone. But given the long series of specimens and its apparent differences with *C. ordinatus* (the only other species of the *C. ordinatus* group in Tasmania), it was considered best to described this species to encourage "off season collecting" in the hope that conspecific males may someday be obtained.

Ceratomerus maculatus n.sp.

Figs. 59, 70, 82, 83, 90, 102–105

Type material. HOLOTYPE ♂, "AUST[ralia]: NSW[New South Wales]: 7 km E/ Robertson, Macquarie Pass/ N.P., 23.xi.1993, cascading/ stream, B.J. Sinclair"; "HOLOTYPE/ *Ceratomerus*/ *maculatus*/ Sinclair [red label]" AMS K175250. PARATYPES: **Australian Capital Territory**: 1♂, 2♀♀, Black Mtn, MT, xii.1987, M. Irwin; 1♂, Blundells Ck, 3 km E Piccadilly Circus, 35°22'S 148°50'E, 850 m, x.1985, Weir, Lawrence, Johnson; 1♀, same locality, v.1988, DHC (ANIC); 5♂♂, 1♀, Gibraltar Falls, 35°29'S 148°56'E, 8.xii.1993, BJS (ZFMK). **New South Wales**: 5♂♂, 3♀♀, same data as holotype; 9♂♂, 7♀♀, Kosciusko NP, Leatherbarrel Ck, 1000 m, 28.xi.1994, BJS, DJB (AMS, ZFMK); 6♂♂, 2♀♀, Barrington Tops NP, upper Gloucester R./Falls, 1200 m, 20–21.xii.1993, BJS (CNC, ZFMK); 2♂♂, Barrington Tops NP, Gloucester Tops, 1200 m, *Nothofagus*, str., 21.xii.1993, BJS; 1♂, Blue Mtns NP, Blackheath, Rim Tr. at falls, 1000 m, 12.xii.1998, BJS; 7♂♂, 1♀, Blue Mtns NP, Grand Canyon, Greaves Ck, 27.iii.1994, 4.iv.1994, 18.vii.1994, BJS; 1♂, Belmore Falls, 2.x.1938, A.L. Tonnoir; 1♂, 5 mi S Monga, tree fern gully, leaf mould, 8.v.1968, DHC & Z. Liepa (ANIC); 4♂♂, Blue Mtns NP, Blackheath, Govett's Ck below falls, 1.xii.1993, 25.xii.1993, 18.vii.1994, BJS; 2♂♂, Blue Mtns NP, Wentworth Falls, 23.x.1994, 10.vii.1994, BJS; 2♂♂, 27♀♀, Gloucester Tops, 1280 m, *Nothofagus*, MT, 19.xi–4.xii.1988, DJB; 1♀, Kanangra-Boyd NP, Boyd R. Cpgd, 1200 m, dry scler. veg., y.pans, 26.xi.1994, DJB; 8♂♂, 12♀♀, Kosciusko NP, upper Pipers Ck, 1600 m, 28–29.xi.1994, 7.xii.1994, BJS; 1♂, Oberon, Silent Ck, 34°6'S 149°45'E, 3.xi.1998, J. Potts; 1♂, Royal NP, Couranga Tr., 19.iii.1995, BJS; 1♂, Katoomba, 28.ix.1955, G.H. Hardy (AMS); 4♂♂, 1♀, Blue Mtns NP, Valley-of-the-Waters, below Vera Falls, 10.vii.1994, 23.x.1994, 9.iv.1995, BJS (AMS, CNC); 2♀♀, Kosciusko NP, nr Swamp Plain, Bogong Ck, 28.xi.1994, BJS; 2♂♂, Monga SF, 19–24.i.1984, L. Masner; 1♂, Royal NP, Uloola Falls, 17.xii.1993, BJS (CNC); 4♂♂, 8♀♀, Styx R. SF, George's Ck F.Res., Cunnawarra Ck, 3.iii.1995, BJS (USNM); 1♀, Styx R. SP, Wattle Flat, Styx R., 1200 m, 1.iv.1995, BJS (ZFMK). **Victoria**: 1♂, Errinundra Plateau, y.pans, Bonang Ck, 1.iv.1990, DJB; 2♂♂, 9♀♀, Errinundra Plateau, Gap Rd, Result Ck Falls, y.pans, 6–7.xii.1994, BJS, DJB; 3♂♂, 5♀♀, 45 km N Orbost, Bonang Hwy, Martins Ck, 200 m, rainfor., 6.xii.1994, BJS; 1♀, Otway NP, Maits Rest, rainfor., y.pans, 350 m, 4–5.xii.1994, DJB; 1♂, 7♀♀, 9 km N Warburton, *Nothofagus*, Cement Ck, 1–3.xii.1994, BJS, DJB (AMS); 1♂, Fern Tree Gully NP, 20.viii.1967, T. Weir (UQIC); 4♂♂, 7♀♀, Otway Ra., *Nothofagus*, Beauchamp Falls, 350 m, 3–5.xii.1994, BJS, DJB (AMS, CNC); 1♀,



Figs. 80–87. Wings of *Ceratomerus*. 80, *C. falcatus*, male. 81, *C. hibernus*, female. 82–83, *C. maculatus*: 82, male; 83, female. 84, *C. ordinatus*, male. 85, *C. albistylus*, male. 86, *C. lobatus*, male. 87, *C. orientalis*, male. Scale bars = 0.5 mm.

Sassafras, 22.x.1922, A. Tonnoir; 3♂♂, 1♀, Warburton, Cement Ck, 670 m, *Nothofagus*, 10–17.i.1980, A. Newton & M. Thayer (ANIC); 6♂♂, 6♀♀, 29 km N Warburton, Acheron Way, Acheron R., rainforest, y.pans, 1–3.xii.1994, BJS, DJB (AMS, CNC); 1♂, Warburton Rd to Mt. Donna Buang, roadcut seep, 3.xii.1994, BJS (CNC).

Additional material (in alc.). **Australian Capital Territory**: 11♂♂, 30♀♀, Blundells Ck, 3 km E Piccadilly Circus, 35°22'S 148°50'E, 850 m, iii–iv.1984, vi.1985, Weir, Lawrence, Johnson; 4♂♂, Wombat Ck, 6 km NE Piccadilly Circus, 35°19'S 148°51'E, 750 m, iv.1984, Weir, Lawrence, Johnson. **New South Wales**: 1♂, 6♀♀, New England NP, Toms Cabin, 30°30'S 152°24'E, 12–22.ii.1984, MT, I.D. Naumann (all ANIC).

Diagnosis. Distinguished by the unique and distinctly bizarre male wing and inwardly bowed hindlegs. Females are generally larger in size than *C. falcatus* with darker wings, however they can be only confidently identified in association with males.

Description. Wing length 2.6–2.9 mm, similar to *C. falcatus* except as follows:

Male. *Head*. Face yellowish-brown; postocellar bristle long, subequal in length to ocellar bristle. Antenna with (Fig. 59)

pedicel nearly equal in length to scape, bearing pair of dorsal setae on distal half; 1 ventral seta and apical fringe of long setae; postpedicel 1.5× height of head; apical three-fifths narrow, nearly parallel-sided, not strongly tapered; three-segmented stylus one-fifth length of postpedicel. Palpus yellow.

Thorax. Pleura yellow, dorsal margin yellowish-brown; postpronotal lobe yellowish-brown.

Wing (Fig. 82) with posterior margin of stem bearing fringe of long dark setae; anal lobe with fringe of minute setulae. Wing venation highly modified: R_1 ending in costa before middle of wing; R_{2+3} and R_4 thickened, highly undulated; base of R_4 thickened; auxiliary cross-vein between R_{2+3} and R_4 absent; 3 veins arising from cell dm; Cu thickened. Costal cell darkly infuscate; cell r_1 with dark spots along margin of R_1; cell br with median streak.

Legs. Coxae and femora yellow, hind femora darker towards tip; tibiae and tarsi brown. Fore femur swollen, with av row of dark setae; pv region with 3 basal setae. Fore tibia equal in length to femur. First tarsomere half length of fore tibia; distal 4 tarsomeres dorsoventrally flattened, ventral margin with bare pale surface.

Mid femur swollen, similar to fore femur, with av row of short setae, longer at base. Mid tibia with triangular lobe subapically, with shallow ventral excavation; apex with tuft of ventral setae. First tarsomere slightly bent subbasally, with stout ventral basal seta; shorter than remaining 4 tarsomeres; fourth and fifth tarsomeres dorsoventrally flattened.

Hind femur bow-legged, with 1 preapical dorsal seta. Hind tibia bent and slightly twisted, compressed near mid-length (Fig. 90); shorter than femur, apex dilated, bearing posteroapical comb; pv surface lacking setae. Hind tarsomeres shorter than tibia, slender.

Abdomen as in *C. falcatus*.

Terminalia (Figs. 102, 103). Hypandrium with short posterior flap-like process; 1 pair of long, sickle-shaped, articulated postgonites flanking phallus. Phallus comprising pair of long, straight, slender processes, overlapping apically. Apical corner of epandrium narrow; posterior margin with long setae along inner posterior margin. Surstylus weakly developed, with only partial subapical weakening on epandrium with row of marginal setae. Cercus thinly sclerotized, short, apex acute, expanded laterally around anus.

Female. Similar to male and female of *C. falcatus* except as follows: wing (Fig. 83) lacking modified venation; darkly infuscate, with pale median streak in cells r_1, r_{2+3} and r_4; medial fork distal to radial fork; cell dm rectangular, slender; auxiliary crossvein between R_{2+3} and R_4 (occasionally absent on one wing). Terminalia (Fig. 104): T10 with anterior margin bearing stout, straight, spine-like setae; cercus with terminal cluster of 4–5 spine-like setae, similar to T10. Spermathecal receptacle spherical (Fig. 105).

Distribution. This species is confined to the southeastern corner of Australia (i.e., southern NSW and Victoria), and overlaps with its sister species, *C. falcatus*, at Barrington Tops National Park and Styx River region in central NSW (Fig. 70). It is found at both high and low altitudes south of Sydney, but restricted to above 1000 m north of this latitude.

Biology. A teneral specimen from the region of Monga was collected among leaf mould in a tree fern gallery. This may indicate that this species (and possibly others of this group) breed in damp soils associated with streams and is thus not truly aquatic.

Etymology. The species name is derived from the Latin *maculatus* (spotted, stained) in reference to the spotted and patterned male wing.

Ceratomerus ordinatus Hardy

Figs. 60, 84, 89, 94, 101, 106–109

Ceratomerus ordinatus Hardy, 1930: 247.
Ceratomerus ordinarius Hardy, 1930: 245.

Type material. NEOTYPE (here designated) ♂, "AUST[ralia]: TAS[mania]: Lyell/ Hwy. Franklin/ Gordon/ Wild Rivers N.P./ 20.ii.1994, Nelson R./ B.J. Sinclair" AMS K175254. My neotype label "NEOTYPE/ Ceratomerus/ ordinatus Hardy/ des. B.J. Sinclair 2000 [red label]" has been attached to this specimen.

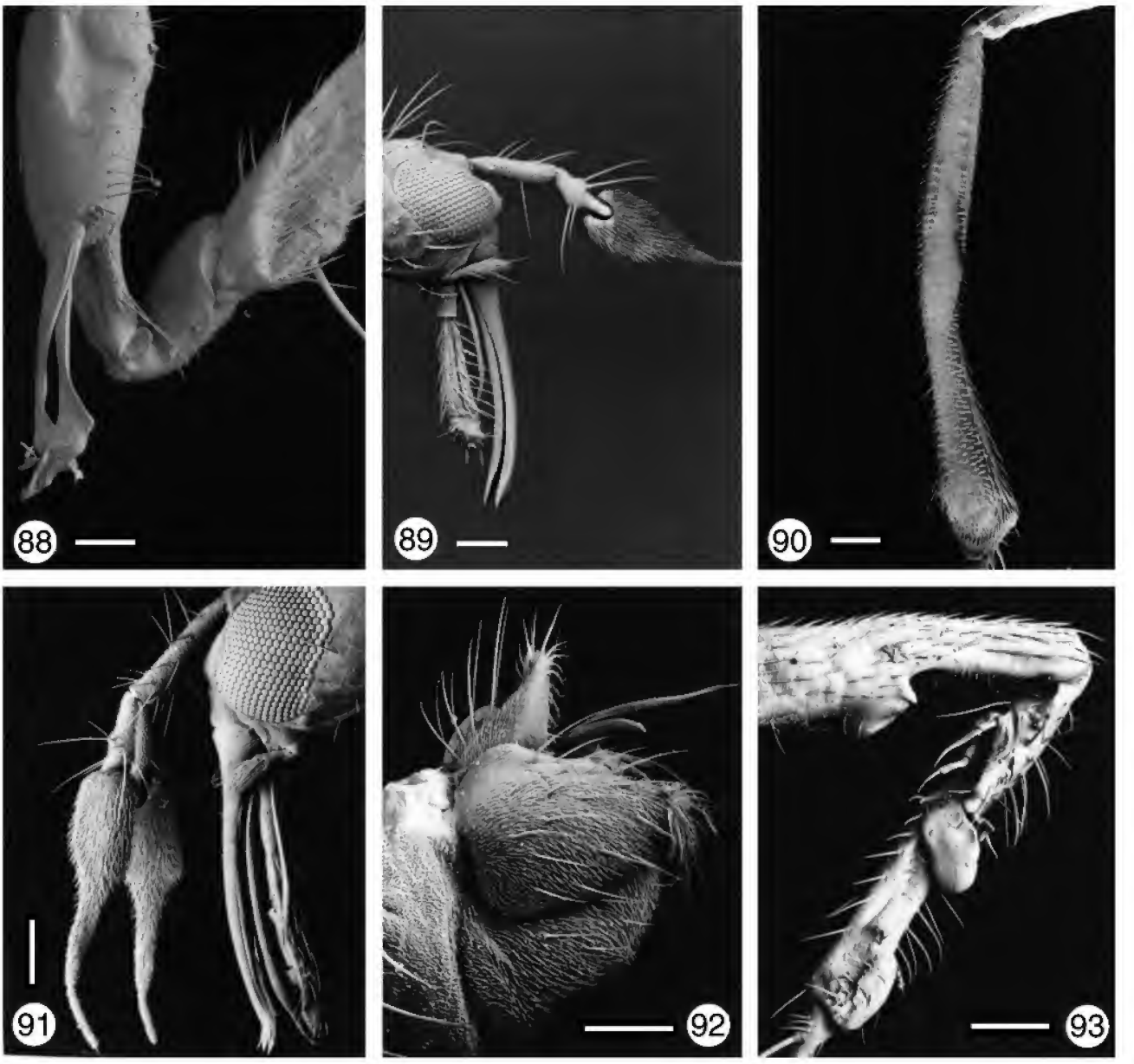
The holotype is lost as discussed previously for all Hardy species of Ceratomerinae and *C. ordinatus* was not mentioned in the list of damaged hardy types by Daniels (1978). The association of all additional material is based on the original description of the wing venation, where the radial and medial veins fork nearly in parallel. The description by Hardy (1930) of the hypopygium as "very large" is considered incorrect and likely confused with *C. inflexus*. In order to avoid misidentifications with other closely related species in Tasmania (e.g., *C. hibernus*), and given the inaccuracies of the original description which may lead to future misidentifications, the designation of a neotype was deemed necessary.

Notes on spelling. This species was first spelt as *ordinarius* in the key to species of *Ceratomerus* (Hardy, 1930), but was subsequently spelt *ordinatus* in the description of the species, Zoological Record, and Smith (1989). As first reviser (I.C.Z.N. 1999, Sec. 24.2.3), I have chosen to accept the second spelling (*ordinatus*) to maintain stability.

Additional material. Tasmania: 8♂♂, 8♀♀, same data as neotype (AMS, ZFMK); 6♂♂, 1♀, Adventure Bay, 30.xii.1922; 1♂, 1♀, Cradle Mtn, 23.v.1923; 2♂♂, 1♀, Cradle Val., 23.i.1923; 1♂, Interview R., N. of Pieman R., 31.xii.1953; 2♂♂, 8♀♀, Pelion Hut, 3 km S Mt. Oakleigh, 860 m, 41°50'S 146°03'E, 8.i., 6–11.iii., 9.iv–6.vi.1991; 1♂, 15♀♀, Pelion Plains, 1.iii., 15.v., 7.vi., 7.xi.1990 (ANIC); 1♀, Arve R., nr Hartz Mtn Rd, y.pans, river rocks, 22–23.i.1989; 30♂♂, 8♀♀, nr Cradle Mtn, Pencil Pine Ck, 800 m, high woodlands, 30.i.1989, y.pans; 1♂, Franklin R., Irenabyss Camp, 11.iii.1989, y.pans; 1♀, Picton Rd, Farmhouse Ck, *E. obliqua* for., y.pans, 43°15'S 146°38'E, 22–23.i.1989 (AMS); 1♂, St. Colomba Falls, Pyengana, 21.ii.1971 (MVM); 1♂, Tahune FR, Huon R., 17.ii.1994 (AMS); 8♂♂, 5♀♀, Cradle Mtn. NP, Pencil Pine Ck, 800 m, 20–22.ii.1994; 4♂♂, 13♀♀, Lyell Hwy, Franklin/Gordon Wild Rivers NP, Franklin R., 19.ii.1994; 4♂♂, 2♀♀, same locality, Surprise R. 19.ii.1994; 1♂, 2♀♀, Mt. Field NP, Lady Barron Falls, 17.ii.1994; 3♂♂, 6♀♀, Rd.C405, 12 km N of C401, 23.ii.1994, small ck (CNC); 4♂♂, 2♀♀, Cradle Mtn. NP, Overland/Dove Lk. Tr., 900–1100 m, 21.ii.1994; 2♂♂, 7♀♀, Mt. Field NP, Russell & Horseshoe Falls, 200 m, 18.ii.1983; 1♂, 2♀♀, same locality, Lk. Dobson, small str. inflow, 1020 m, 18.ii.1984 (ZFMK); 1♂, 20 km SW Derwent Bridge, Franklin, 11.ii.1971 (MVM); 1♂, 1♀, Franklin R., 42°13'S 146°01'E, 22.i.1983, at light (ANIC-alc.); 1♂, 15 km W Geeveston, Keoghs Ck, 17.ii.1994 (USNM); 5♂♂, 5♀♀, Hellyer Gorge, 2.ii.1967, 9.ii.1971 (ANIC, MVM); 7♂♂, 2♀♀, Myrtle Bank, St. Patricks R., 22.ii.1994 (CNC, ZFMK).

Diagnosis. Distinguished from others in this group by a shortened pedicel (one-fourth length of scape) and median fork separated from radial fork by less than the length of crossvein dm-cu.

Description. Wing length 2.5–2.8 mm, similar to *C. falcatus* except as follows:



Figs. 88–93. Scanning electron micrographs of *Ceratomerus*. 88, *C. campbelli*, male fore coxa, inner view. 89, *C. ordinatus*, female head, lateral view. 90, *C. maculatus*, male hind tibia, posterior view. 91–92, *C. falcatus*: 91, male head, lateral view; 92, male terminalia, lateral view. 93, *C. albistylus*, male midleg, anteroventral view. Scale bars = 0.1 mm, except Fig. 92 where scale bar = 0.05 mm.

Male. *Head* (Fig. 89) including face dark brown; postocellar bristle slightly shorter than ocellar bristles; 3 pairs of long vertical bristles. Antenna with scape equal to height of eye, with 2–3 long, dorsal setae and 1 long ventral seta (Fig. 60); pedicel with short basal section, one-fourth length of scape, with posterior fringe of long setae. Postpedicel with apical half strongly tapered to short, stout, three-segmented stylus, subequal to one-third length of postpedicel.

Thorax. Mesonotum, pleura and postnotum dark brown. Antepronotum with 2 short setulae.

Wing (Fig. 84). Medial fork branching nearly opposite radial fork, separated by less than length of crossvein dm-cu.

Legs. Coxae and basal half of femora yellowish-brown, remaining leg segments brown, gradually darkening towards tip. Fore femur slightly swollen, lacking modified ventral setae; bearing 1 erect, preapical dorsal seta. Fore tibia nearly equal in length to femur. First tarsomere slightly longer than half length of fore tibia; distal 4 tarsomeres slender, longer than first tarsomere.

Basal half of mid femur with biserial row of short setae beneath; bearing, 1 erect preapical dorsal seta. Mid tibia slightly shorter than femur lacking modified setae; bearing 1 preapical ad seta. First tarsomere shorter than remaining 4 tarsomeres, with several erect stout setae beneath.

Hind tibia longer than femur; apical half with 4–5 erect ad and 2–3 dorsal setae (Fig. 94).

Abdomen as in *C. falcatus*.

Terminalia (Figs. 106, 107). Hypandrium with short posterior flap-like process; gonocoxal apodemes slender, not projecting beyond base of hypandrium; 2 pairs of articulated postgonites arching in opposite directions. Phallus comprises 1 pair of long, slender, nearly straight processes and thinly sclerotized, ragged-edge median process. Apical corner of epandrium narrow; posterior margin with long setae and short, stout spine-like setae along inner posterior margin. Surstylus weakly developed, with only partial subapical lateral

weakening on epandrium. Cercus thinly sclerotized, short, fleshy; apex acute, expanded laterally around anus.

Female. Similar to male and female of *C. falcatus* except as follows: Terminalia (Fig. 108): anterior margin with broad, flattened, median process, extending beneath T7 when segment retracted (Fig. 109). Anterior margin of T10 bearing biserial row of stout, straight spine-like setae; cercus with terminal cluster of 4–5 spine-like setae, similar to T10. Spermathecal receptacle spherical, with short ridge where duct attached.

Distribution. This species is endemic to Tasmania, with adults commonly collected throughout both eastern and western areas of the island (Fig. 101) from November to May.

Ceratomerus sp. (undescribed)

Material examined. ♀, **Philip Island** (nr. Norfolk Is.) 29°07'S 167°57'E, Upper Long Valley, 26.iii–2.iv.1984, MT, D.C.F. Rentz (ANIC).

Diagnosis. This female specimen is in very poor condition and consequently not described. It appears to be most closely related to *C. falcatus* and *C. maculatus* on the basis of wing venation and lengthened pedicel.

Diagnosis. Female with wing length 2.5 mm. Pedicel cylindrical, slightly greater than half length of scape; radial fork proximal to medial fork; cell dm rectangular, slender; auxiliary crossvein between R_{2+3} and R_4 present.

Biology. This specimen was collected on Philip Island, which lies about 6 km south of Norfolk Island (Rentz, 1989). This island is ecologically devastated, primarily the result of the introduction of rabbits which striped the island of vegetation and caused widespread erosion (Rentz, 1989, figs. 4–9). This species of *Ceratomerus* has surprisingly survived the changes to this island in narrow damp valleys protected by low shrubs. As discussed in "Biology" under *C. maculatus*, it is hypothesized that this species group breeds in damp soil near streams. Thus the breeding habitat of this species has remained protected in the narrow sheltered valleys.

Unplaced Australian species

Although the following species are considered to be most closely related to other Australian species, they could not be confidently assigned to a particular Australian species group. They remain problematic, especially *C. albistylus* which differs greatly from all other Australian species.

Ceratomerus albistylus Hardy

Figs. 61, 62, 85, 93, 95, 96, 110–112, 118

Ceratomerus albistylus Hardy, 1930: 246; Smith, 1989: 387.
C. albistilus Hardy, 1930: 245, 246 (mis-spelling).
C. tuberculus Hardy, 1930: 247; Smith, 1989: 387.

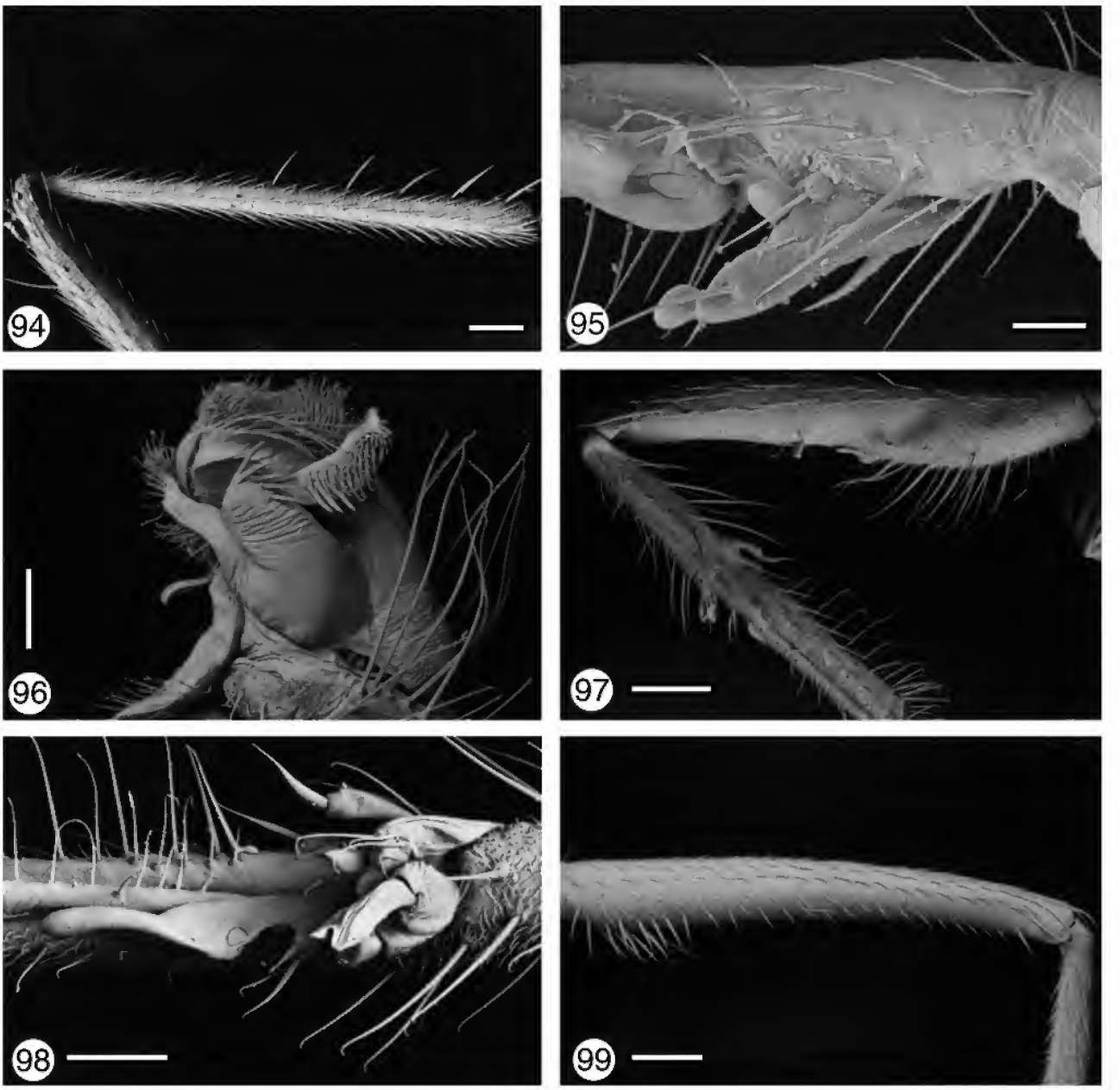
Notes on spelling and synonymy. *Ceratomerus albistilus* was spelt originally as such by Hardy (1930) in both his key and description, but was spelt *albistylus* when compared to another species (*C. ordinatus*) taken at the same locality. This species was subsequently spelt *albistylus* in the Zoological Record and Smith (1989). As first reviser (I.C.Z.N. 1999, Sec. 24.2.3), I have chosen to maintain the spelling as used by Smith (1989) in order to avoid further confusion.

The description of *C. albistylus* was based only on female specimens and *C. tuberculus* on males. On the basis of similar colour patterns Smith (1989) synonymized these two species and I can confirm this nomenclatural change.

Type material. NEOTYPE (here designated) ♂, "Mt. Wellington/ Tas[mania, Australia]/ 12 Feb. 1963/ D.H. Colless"; "Wet forest/ (lower slopes) [dissected]" (ANIC). My neotype label "NEOTYPE/ Ceratomerus/ albistylus Hardy/ des. B.J. Sinclair 2000 [red label]" has been attached to this specimen.

The syntypes of *C. albistylus* (type localities: Mt. Wellington, Strahan and Cradle Mountain) and *C. tuberculus* (type locality: Mt. Wellington) were not located and are presumed destroyed as discussed under *C. inflexus*. No specimens of these species were mentioned in the list of damaged Hardy types by Daniels (1978). The male specimen selected as neotype agrees with the original description and is from the same locality as the original material described by Hardy. The designation of a neotype clearly establishes the identity of this species.

Additional material. Australian Capital Territory: 2♀♀, Blundell's, 13.xi.1938 (ANIC). **New South Wales**: 2♂♂, 2♀♀, Belmore Falls, 23.i.1963; 8♂♂, 8♀♀, Brown Mt., Rutherford Ck, 10.iii., 11.xi.1961; 2♀♀, Bulli, Cataract Ck, 2.xi.1960; 2♂♂, 1♀, Clyde Mt., Landslip, 22.ii.1965; 1♂, Fitzroy Falls, 22–27.xi.1937; 2♂♂, 1♀, Kangaroo Valley, west slope, 23.xi.1960; 1♂, 2♀♀, Macquarie Falls, 14.xi.1960, 13.x.1986; 3♀♀, New England NP, Point Lookout, 30°29'S 152°25'E 12.ii.1984 (ANIC); 5♂♂, 1♀, Blue Mtns NP, Blackheath, Popes Glen, dry scler. for., 31.x.1994; 2♂♂, 1♀, Blue Mtns NP, Grand Canyon, rainfor., 25.xii.1993 (ZFMK); 1♀, Blue Mtns NP, below Govett's Leap, 7.xii.1956; 1♂, 1♀, Gloucester Tops, *Nothofagus*, 1290 m, 14.xi–4.xii.1988; 2♂♂, 3♀♀, Minnamurra Falls, 7.i., 20.x.1961; 1♂, Mt. Dromedary, summit, 800 m, rainfor., 9.xi.1985; 1♂, Nadgee SF, Maxwell's Ck, warm temp. rainfor., 400 m, 13–19.ii.1987; 2♂♂, New England NP, Thungutti Rest A., *Nothofagus*, 20–22.xii.1994; 1♀, New England NP, Wright's Lookout, 1.iv.1961; 2♂♂, Werrikimbe NP, Cobcroft Ck, 1110 m, 6.xii.1986 (AMS); 5♂♂, 19♀♀, Blue Mtns NP, Mt. Wilson, rainfor., Waterfall Ck, 19.xi.1921, 5.xii.1956, 28.xi., 11.xii.1959, 30.xii.1960, 5.xi.1977, 23.xi.1982, 8.xii.1986, 10.xi.1990, 22.xi.1993, 12–13.xii.1998 (AMS, ANIC, CNC, ZFMK); 1♀, New England NP, Toms Cabin, 30°30'S 152°24'E, 12–22.ii.1984 (ANIC-alc.); 3♂♂, Wentworth Falls, Jamison Ck, 4.xii.1956, 10.xi.1993 (AMS, CNC). **Tasmania**: 6♀♀, same data as neotype; 2♀♀, Adventure Bay, 18, 20.xii.1922; 1♂, 2♀♀, Cradle Valley, 12–16.ii.1923; 4♀♀, 9 km WSW Derwent Bridge, 42°10'S 146°08'E, 21.i.1983; 2♀♀, King River, 4.ii.1923; 1♀, Mt. Field NP, Russell Falls, 23.ii.1967; 2♀♀, National Park, 15–16.xii.1922; 4♂♂, 5♀♀, 5 km ESE Redpa, 42°57'S 144°49'E, 18.i.1983; 1♀, Lk. Margaret, 3.ii.1923; 2♂♂, 2♀♀, 10 mi E Strahan, 7.ii.1967 (ANIC); 1♀, Arthur Plains, 3.ii.1965; 1♀, Sir John Falls, Cataract Ck, trib. Gordon R., 9.i.1977; 2♀♀, Tasman Peninsula, Pirates Ck, 2.5 km SW Eaglehawk, 13.ii.1990 (MVM); 10♀♀, Arve R. nr Geeveston, 20.i.1960; 6♀♀, Arve R. nr Hartz Mtn Rd., river rocks, 22–23.i.1989, y.pans; 1♂, 1♀, Corinna, 8.i.1960; 1♀, 16 mi NE Cradle Mtn, 2200 ft, 5.i.1960; 2♀♀, Ferntree nr Hobart, 12.i.1960; 1♀, Junee Caves, nr Maydena, 13.i.1960; 1♀, Lyell Hwy, Double-Barrel Ck, rainfor., y.pans, 27.i.1989; 1♂, 6♀♀, Lyell Hwy, Franklin R. Crossing, 16.i.1960; 8♀♀, Marakoopa Caves, nr Mole Ck, 10.i.1960; 6♀♀, Mt. Barrow, 25–3000 ft, 24–25.i.1960; 4♀♀, Mt. Field NP, Lady Barron Ck, 900 m, y.pans, subalpine, 25.i.1989; 1♀, 2 mi S Oonah, Waratah Hwy, 7.i.1960; 1♀, Scotts Peak Dam Rd & Clear Ck, wet scler., MT, 4–5.ii.1989; 1♀, Tasman Peninsula, Long Bay Ck, wet scler., y.pans, 7–9.ii.1989; 3♀♀, Zeehan-Renison Bell SR, N. Zeehan, rainfor., 28.i.1989 (AMS); 7♀♀, Eaglehawk Neck, 17–22.xi.1922, 17.i.1960; 8♀♀, Hellyer R. Gorge, S. Wynyard, rainfor., 2–3.ii.1967, 29.i.1989 (AMS, ANIC); 4♀♀, Lyell Hwy, Franklin/Gordon Wild Rivers NP, Surprise R. 19.ii.1994 (CNC); 15♀♀, Pelion Hut, 3 km S Mt. Oakleigh, 860 m, 41°50'S 146°03'E, 5–10.ii.1990, 8.i–12.ii.1991, 6–11.iii.1991 (ANIC); 2♀♀, Rd C405, 12 km N of C401, small ck, 23.ii.1994 (ZFMK); 1♀, Rosebery, ii.1977 (BPBM); 1♀, 4 km E Rosebery, 41°47'S 145°35'E, MT, 16.i–



Figs. 94–99. Scanning electron micrographs of male *Ceratomerus*. 94, *C. ordinatus*, hind tibia, anterior view. 95–96, *C. albistylus*: 95, mid tibia, anterior view; 96, terminalia, lateral view. 97–98, *C. lobatus*: 97, midleg, oblique posterior view; 98, mid tibia, ventral view. 99, *C. orientalis*, mid femur, anterior view. Scale bars = 0.1 mm, except Figs. 95, 98 where scale bars = 0.05 mm.

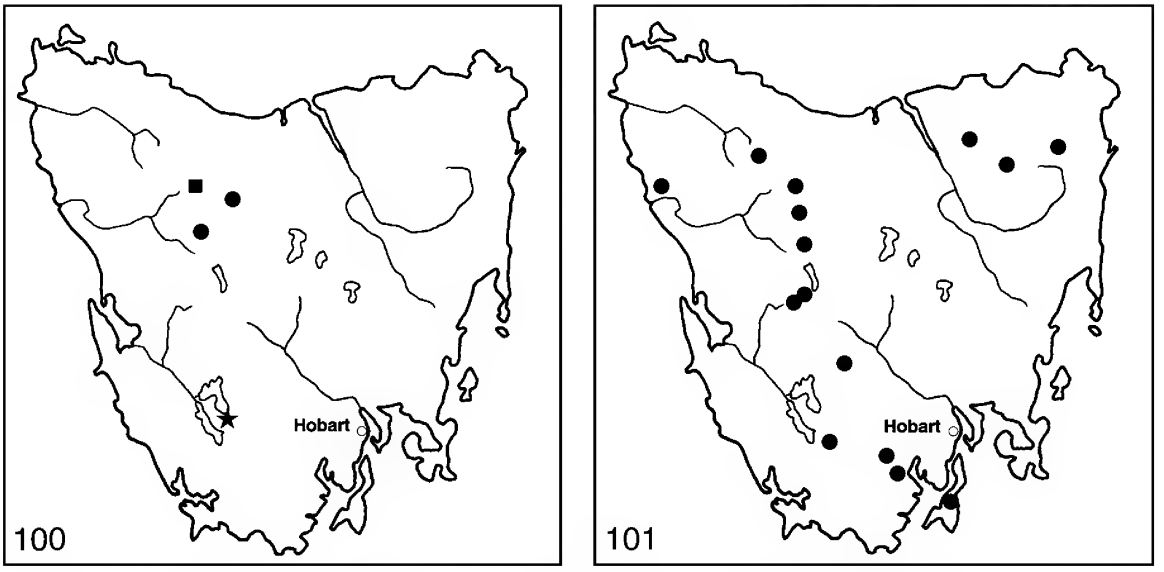
1.ii.1983; 1♀, 42°43'S 145°49'E, rainfor, 3.ii.1978 (ANIC-alc.). **Victoria**: 9♂♂, 5♀♀, Acheron Ck, 29 km from Warburton, y.pans, 400 m, 1–3.xii.1994 (AMS, ZFMK); 1♀, 10 mi E Beech Forest, 1.i.1967; 1♂, Cabbage Tree Ck, 18.xi.1964; 2♂♂, Nowa Nowa, 28.x.1961; 1♂, Spring Hill Junction, 9 mi N Dargo, 4000 ft, 13.ii.1965 (ANIC); 1♂, Belgrave, 20.i.1930; 1♀, 8 km SSW Gellibrand, Upper Carlisle R., 27.i.1982; 1♂, Noorinbee, 12.xi.1969 (MVM); 1♂, Donna Buang Rd, 15.xii.1970 (ANIC-slide); 14♂♂, 5♀♀, Errinundra Plateau, Result Ck Falls & Gap Rd, 900 m, 6–7.xii.1994 (AMS, CNC, ZFMK); 1♀, Grampians NP, Delley's Dell, 4 km SSW Halls Gap, 37°11'S 142°31'E, 30.xi.1992; 1♀, Result Ck & Gap Rd, 920 m, cool rainfor., y.pans, 17.i.1991 (AMS); 2♀♀, NNE Melbourne, 20.xii.1960 (BPBM); 2♂♂, 5♀♀, Otway NP, Maits Rest, temp. rainfor, ck, 4–5.xii.1994 (AMS, ZFMK); 1♀, Otway Ra., Beauchamp Falls, *Nothofagus*, 3.xii.1994; 3♂♂, Otway Ra., Melba Gully SP, temp. rainfor., ck, 4.xii.1994 (CNC); 5♂♂, 2♀♀, 9 km N Warburton, Cement Ck, 27.x.1961, 7.iv.1963, 1–3.xii.1994 (AMS, ANIC, CNC).

Diagnosis. Recognized by its dark, shiny abdomen, bright yellow legs, white tipped female stylus and greatly lengthened male antennae, with inconspicuous stylus.

Description. Wing length 3.7–4.2 mm, similar to *C. attenuatus* except as follows:

Male. *Head* dark brown, shiny, with white pruinescence; ocellar triangle with 2 closely spaced, divergent bristles, inserted between lateral ocelli; postocular bristles very short and fine. Antenna with scape two-thirds height of eye, with many short dorsal setae and 1 long ventral seta (Fig. 61); pedicel with 1 long dorsal seta. Postpedicel greatly lengthened to 3× height of head, gradually tapered; apical stylus very short, inconspicuous. Palpus yellow, slender, one-sixth length of labrum, with several dark setae.

Thorax. Mesonotum and postnotum dark brown, shiny; pleura shiny, proepisternum, anterior portion of anepisternum, and postpronotal lobe yellow; scutum with median vitta of pruinescence; lateral margin of scutum, prescutellar depression and postnotum with patch of pruinescence.



Figs. 100–101. Known distribution of species of *Ceratomerus* (Tasmania). 100, *Ceratomerus bickeli* ★, *C. bulbosus* ■, *C. hibernus* ●. 101, *Ceratomerus ordinatus*.

Alternating row of short acrostichals to prescutellar depression, directed posteriorly; 4 dc, third dc stout and long, with setulae intermixed; 4 sctl, outer pair short, slender. Antepronotum with 2 short setulae.

Wing (Fig. 85). Single short costal seta. R_{2+3} not deflected around stigma; radial fork bell-shaped; stem of median fork sometimes nearly twice length of crossvein dm-cu; medial fork proximal to radial fork by less than length of R_4. Halter with yellow knob.

Legs. Coxae, femora and tibiae bright yellow, hind femur darker towards tip; tarsi becoming dark towards tip. Fore coxa less than twice length of mid coxa. Fore femur slender, with av row of dark slender setae. Fore tibia nearly equal in length to femur. First tarsomere subequal in length of fore tibia; distal 4 tarsomeres slender, subequal in length to first tarsomere.

Apical third of mid femur strongly constricted with posterior projecting lip; 1 long av and 2 long pv setae near mid-length. Mid tibia with projecting appendage corresponding to constriction on femur; appendage with spherical apex and subapical seta (Fig. 95); pad-like swelling at mid-length and apex of tibia (Fig. 93). First tarsomere longer than remaining 4 tarsomeres, with long curved ventral seta at base.

Hind femur often with long preapical av setae. Hind tibia longer than femur, apex slightly dilated, bearing postero-apical comb; apical half with several erect ad setae; long, slender erect setae often present beneath.

Abdomen shiny, dark brown, T1–5 with short postero-marginal setae; T6 with long posteromarginal setae; T7 pale; S7 slightly longer than preceding sternite; T8 with narrow, posterior incision; posteromargin of S8 with long, stout setae, often extending beyond terminalia.

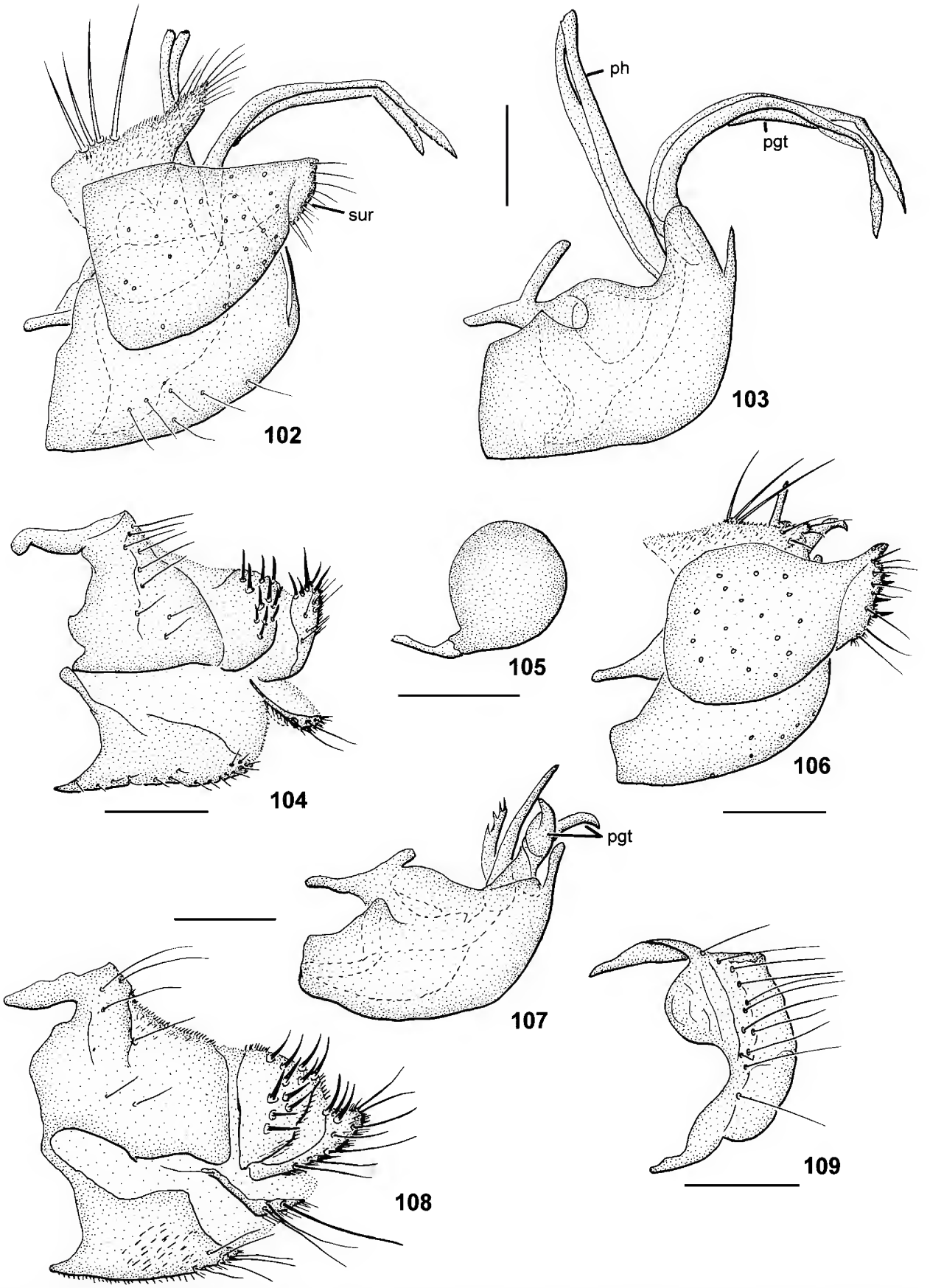
Terminalia (Figs. 96, 110, 111). Hypandrium with long posterior flap-like process; postgonites sickle-shaped, with twisted, hooked tips; posteromargin with fringe of long setae, often stout. Phallus with pair of strongly arched processes, curving around flanking postgonites. Postero-apical margin of epandrium with patch of spine-like setae; epandrial lobe slender, with sparse setal fringe and dense crown of setae. Surstylus long and slender, with posterior fringe of dark, stout setae. Cercus thinly sclerotized, short, apex acute, expanded laterally around anus; posterior margin thickly sclerotized.

Female. Similar to male and female of *C. attenuatus* except as follows: palpus brown. Postpedicel more strongly attenuated (Fig. 62), with apical fourth white. Halter dark. Lateral margin of S7 straight. Terminalia (Fig. 112): anterior half of T10 with several rows of stout, curved spine-like setae; cercus with row of short spine-like setae, similar to T10. Spermathecal receptacle spherical, with short ridge-like neck where duct attached.

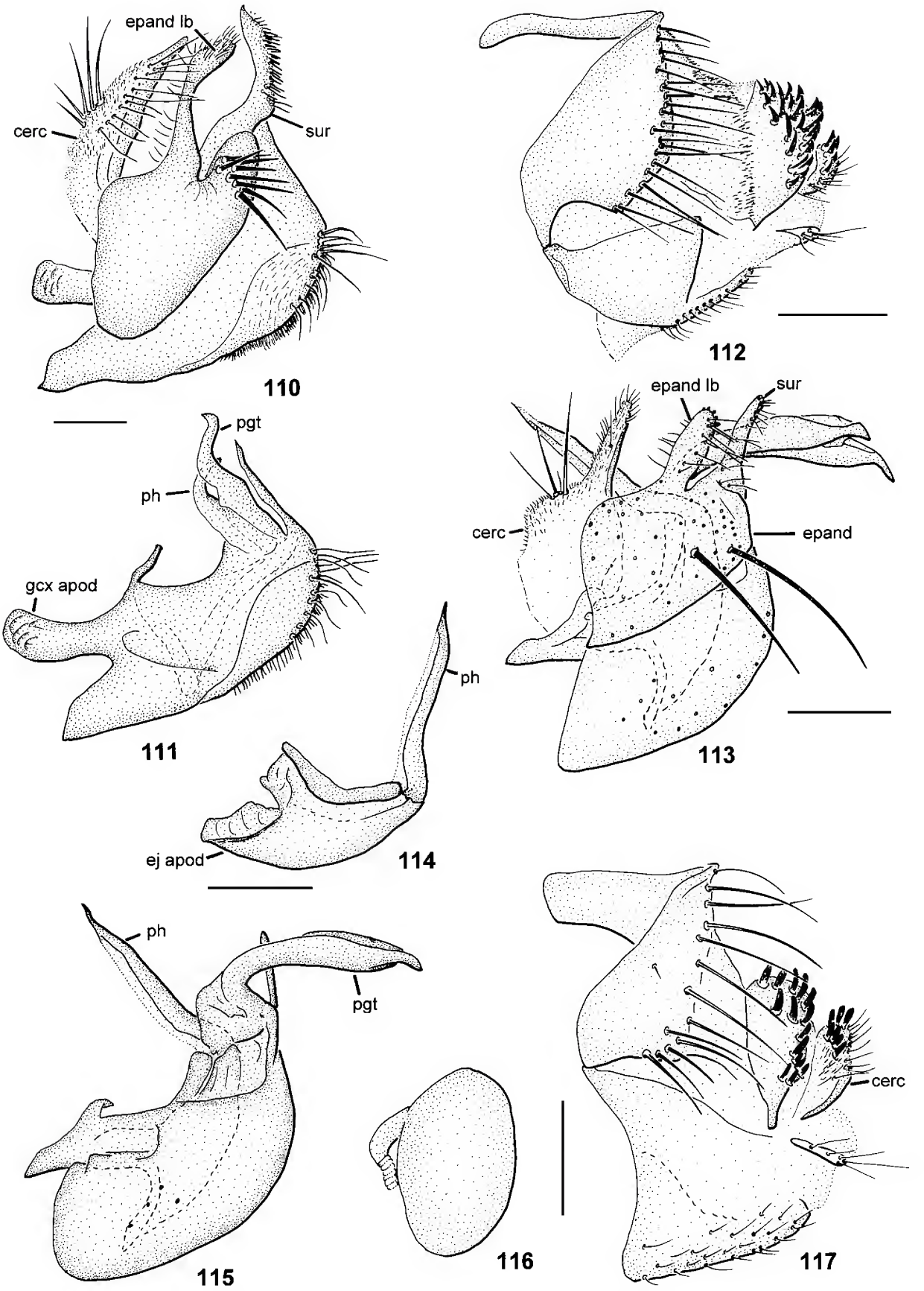
Distribution. Widespread in southeastern Australia, this species is known from throughout Tasmania, westward to the Grampians in Victoria and north to New England National Park in northern New South Wales (Fig. 118). Most common at southern latitudes, and confined to higher elevations north of Sydney.

Biology. This species is commonly collected by sweeping riparian vegetation and rarely swept from emergent rocks in streams. Occasionally specimens are found quite distant from running water.

Remarks. Three differing morphological forms can be somewhat identified. Populations in Victoria (Warburton/Cement Creek region and Otway Ra.), can be distinguished by the absence of a posteromarginal fringe of setae on the hypandrium, and presence of long, slender setae on the apical fourth of the male hind femur and ventral region of the male hind tibia. A northern population is also distinguishable, ranging from Gloucester Tops north. This population is distinguished by the very stout setal fringe on the hypandrium, and the hindlegs also possess long erect setae as in the form known from Victoria. The typical form (widespread, ranging from Tasmania, Victoria and southern NSW), possesses a long setal fringe on the hypandrium and lacks long, slender setae on the male hindlegs.



Figs. 102–109. Terminalia of *Ceratomerus*. 102–105, *C. maculatus*: 102, male, lateral view; 103, hypandrium and phallus; 104, female, lateral view; 105, spermatheca. 106–109, *C. ordinatus*: 106, male, lateral view; 107, hypandrium and phallus, lateral view; 108, female, lateral view; 109, female tergite 8, oblique dorsal view. Scale bars = 0.05 mm, except Fig. 105 where scale bar = 0.1 mm. Abbreviations: *pgt*, postgonite; *ph*, phallus; *sur*, surstylus.

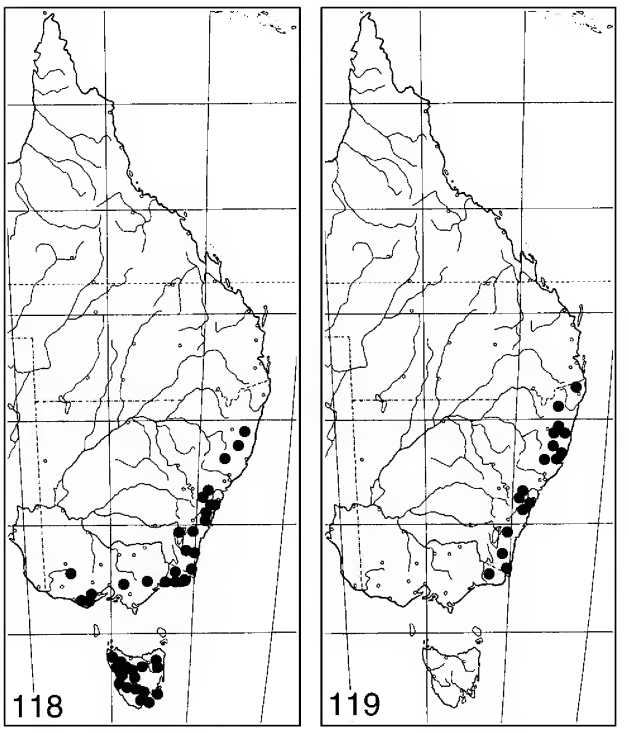


Figs. 110–117. Terminalia of *Ceratomerus*. 110–112, *C. albistylus*: 110, male, lateral view; 111, hypandrium and phallus, lateral view; 112, female, lateral view. 113–117, *C. lobatus*: 113, male, lateral view; 114, phallus, lateral view; 115, hypandrium and phallus, lateral view; 116, spermatheca; 117, female, lateral view. Scale bars = 0.1 mm. Abbreviations: *cerc*, cercus; *ej apod*, ejaculatory apodeme; *epand*, epandrium; *epand lb*, epandrial lobe; *gcx apod*, gonocoxal apodeme; *pgt*, postgonite; *ph*, phallus; *sur*, surstylus.

Ceratomerus lobatus n.sp.

Figs. 86, 97, 98, 113–117, 119

Type material. HOLOTYPE ♂, "AUST[ralia]: NSW[New South Wales]: Blue Mtns/ N.P. Grand Canyon/ 27.iii.1994/ B.J. Sinclair/ ex. Greaves Ck."; "HOLOTYPE/ Ceratomerus/ lobatus/ Sinclair [red label]" AMS K175251. PARATYPES: **New South Wales**: 6♂♂, 4♀♀, same data as holotype (AMS); 4♂♂, 3♀♀, Blue Mtns, NP, Grand Canyon, Greaves Ck, 25.xii.1993, 4.iv.1994, 18.vii.1994, BJS (CNC, ZFMK); 3♂♂, 4♀♀, Blue Mtns NP, Mt. Wilson, 19.xii.1986, DKM, B.J. Day, R. de Keyzer (AMS), 19.viii.1961, DHC (ANIC), Waterfall Ck, 22.xi.1993, BJS; 1♂, 1♀, Blue Mtns NP, Wentworth Falls, Jamison Ck, 10.xi.1993, BJS; 1♂, Border Ranges NP, Brindle Ck, rainfor., 1000 m, 25.i.1995, BJS; 6♂♂, Bruxner Pk FlR, nr Coffs Harbour, Bucca Bucca Ck, 100 m, subtrop. rainfor., 1.iv.1995, BJS; 2♂♂, Royal NP, Wallumarra Tr., Bola Ck, 7.xi.1993, BJS (CNC); 1♂, Blue Mtns NP, Valley of the Waters, Vera Falls, 320 m, y.pans, 9.iv.1995, BJS; 1♂, Dorrigo NP, Rosewood Ck, rainfor., y.pans, 23.i.1995, BJS; 3♂♂, Macquarie Pass NP, 7 km E Robertson, subtrop.for., 23.xi.1993, BJS; 6♂♂, Royal NP, below National Falls, subtrop.for., 29.v.1994, BJS; 3♂♂, Styx R. SF, George's Ck FR, Cunnawarra Ck, 31.iii.1995, BJS; 2♂♂, Royal NP, Couranga Tr., 23.iv.1995, BJS (ZFMK); 3♂♂, 1♀, Brown Mtn, Rutherford Ck, 15.iii.1961, 17.vii.1963, DHC; 7♂♂, 6♀♀, 4 mi S Monga, 8.v.1968, DHC & Liepa (ANIC); 4♂♂, 2♀♀, Carrai SF, Coachwood Ck nr Kookaburra Camp, y.pans, 8–9.ii.1997, DJB; 3♂♂, Dingo Tops For. Pk, NW Wingham, 950 m, rainfor., MT, 20.ii–23.iii.1993, G. Williams; 3♂♂, 2♀♀, Dorrigo NP, Never Never area, Sassafras Ck, temp. rainfor., 750 m, y.pans, 1–2.iv.1995, DJB; 1♀, Ebor, Point Lookout, 5000 ft, 31.iii.1960, DKM; 1♂, 2♀♀, Gloucester Tops, 1280 m, *Nothofagus*, MT, 19.xi–4.xii.1988, DJB; 4♂♂, 2♀♀, Lansdowne SF, Newby's Cave, 24 km N Taree, 300 m, warm temp. rainfor., 20.v.1993, G.&T. Williams; 1♀, Mt. Gibraltar NP, 64 mi W Grafton, 24.ii.1965, DKM; 1♂, Mt. Hyland NP, Obeloe Ck, 1030 m, 30°10'S 152°27'E, warm temp. rainfor., 25–27.i.1996, DJB; 1♀, Nadgee NP, Bruce's Ck wet scler. for., 18–19.ii.1987, DJB; 8♂♂, 2♀♀, Nadgee NR nr Eden, wet scler. for./ Nadgee R., 14–15.ii.1986, 15.ii.1987, DJB; 6♂♂, 7♀♀, Royal NP, Bola Ck, 28.iv.1956, 1.vi.1963, 24.vi.1961, 6.vii.1966, 10.viii.1957, 19.xi.1960, DKM; 1♂, 2♀♀, Washpool NP, Coombadjah Ck, 780 m, warm temp. rainfor., 6.xii.1992, DJB; 4♂♂, Werrikimbe NP, Cobcroft Ck nr Walcha, temp. rainfor., 23.iii.1985, 1–5.xii.1997 DJB (AMS). **Victoria**: 28♂♂, 15♀♀, Errinundra Plateau, Bonang Ck, y.pans, 1.iv.1990, DJB (AMS).



Figs. 118–119. Known distribution of species of *Ceratomerus* (eastern Australia). 118, *C. albistylus*. 119, *C. lobatus*.

Diagnosis. Recognized by the short, distinct stigma, bright yellow-coloured pleura and sculptured mid tibiae with pectinate setae of the male midleg.

Description. Wing length 2.8–3.5 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Postocellar bristles one-third length of ocellar bristles. Antenna with length of scape subequal to height of eye; postpedicel apical two-thirds strongly tapered; three-segmented stylus one-third length of postpedicel; length of segment 8 twice width. Palpus pale, slender, one-fourth length of labrum, with several dark setae.

Thorax. Scutum and postnotum dark brown; pleura bright yellow, except brown laterotergite; postpronotal lobe pale brown.

Wing (Fig. 86). R_{2+3} running parallel and close to costa, smoothly arched around stigma.

Legs. Fore and mid coxae yellow, hind coxa yellowish-brown; base of femora, especially inner margin yellow, becoming dark brown towards tip. Fore coxa nearly twice length of mid coxa. Fore femur slightly swollen, with biserial av row of fine setae, mostly longer than width of femur; 1 weak preapical dorsal seta.

Mid femur more strongly swollen than fore femur, with deep attenuation at mid-length; basal half with cluster of 3 flattened anterior setae and group of basal setae, some nearly subequal in length to width of femur; apical half with short, pointed stud-like process; 1 stout, erect ad seta at apical fourth (Fig. 97). Mid tibia with shallow excavation at mid-length; anterior margin of notch with flattened lobe; basal half with erect, anterior and posterior setae, longer than width of tibia; base of notch with bilobed process, bearing broad flattened seta; ventral margin of notch with 3 cylindrical lobes, bearing stout, wavy seta (Fig. 98); apical half with pv row of setae, shorter than width of tibia; apex with cluster of subapical, anterior setae. First tarsomere longer than remaining 4 tarsomeres (one-third longer than tibia), with many erect pv setae.

Hind femur with av row of short setae.

Abdomen dark brown, concolorous with mesonotum; S7 only slightly longer than preceding sternite, anterolateral margin produced anteriorly; T8 narrow, expanded laterally.

Terminalia (Figs. 113, 115). Hypandrium convex, posterior margin extended as long, flat, median process, reaching beyond postgonites; gonocoxal apodemes developed, just projecting beyond anterior margin; postgonites articulated at base of phallus, strongly recurved posteriorly; phallus upright, straight, tapered to sharp apex (Fig. 114). Epandrium with 2 very long, stout setae arising posterolaterally; epandrial lamellae small, not greatly inflated, fused ventrally to hypandrium at av corner; epandrial lobe anterior to surstylus short and broad, bearing stout, blunt inner apical setae. Surstylus slender, longer than epandrial lobe, with row of marginal setulae; subepandrial plate narrow, lacking extensions and lobes. Cercus slender, fleshy, posterior margin more thickly sclerotized.

Female. Similar to male and female of *C. attenuatus* except as follows: lacking av row of setae of fore femur; mid tibia with 2 erect ad and 1 pd seta on basal half. Posterodorsal corner of anepisternum with more expansive dark colouration. Lateral margin of S7 straight. Terminalia (Fig. 117): T10 bearing row of blunt-tipped, spine-like setae along posterior margin. Cercus bearing row of blunt-tipped, spine-

like setae, with slender marginal setae. Spermathecal receptacle somewhat flattened, oval, with short neck (Fig. 116).

Distribution. This species is restricted almost exclusively to New South Wales, with additional records from northeastern Victoria (Fig. 119). It is widespread in both high and lower altitudes.

Biology. In mountainous regions, this species is found year round. In the streams of gallery rainforests which thread through broad sclerophyll forests around Sydney (e.g., Bola Creek, Royal NP), this species is found primarily in the cooler months, with records from April to November.

Etymology. The specific name is from the Latin *lobus* (an elongated projection), referring to a slender lobe on the male mid tibia.

Ceratomerus orientalis n.sp.

Figs. 29, 87, 99, 120–124

Type material. HOLOTYPE ♂, "AUST[ralia]: NSW[New South Wales]: Royal/ N.P., Bola Creek/ 3.iv.1994/ B.J. Sinclair"; "HOLOTYPE/ Ceratomerus/ orientalis/ Sinclair [red label]" AMS K175252. PARATYPES: **New South Wales**: 1♀, same data as holotype; 5♂♂, 3♀♀, Barrington Tops NP, 350 m, lower Gloucester R., 2.xii.1988, 21.xii.1993, DJB; 1♂, same locality, Upper Williams R., 550 m, 26.i.1987, DJB; 4♂♂, 2♀♀, same locality, Gloucester Tops, 1280–1290 m, *Nothofagus*, 14.xi–30.xii.1988, DJB; 1♂, Blue Mtns NP, Burralow Swamp, 9.xii.1986, G.A. Holloway; 10♂♂, 6♀♀, Blue Mtns NP, Valley of the Waters, Vera Falls, 10.vii.1994, 23.x.1994, 9.iv.1995, BJS; 5♂♂, Carrai SF, Coachwood Ck nr Kookaburra Camp, 8–9.ii.1997, DJB; 7♂♂, 2♀♀, Chichester SF, Upper Allyn R., 400 m, subtrop. rainfor., 19–20.xii.1993, DJB, nr Eccleston, 4.v.1967, DKM; 33♂♂, 8♀♀, Cockerawombeeba Ck, 23 km WNW Bellangry, warm temp. rainfor., 8.xii.1986, 14–15.i.1988, DJB; 5♂♂, 1♀, Comboyne-Wingham Rd, 10 km SSW Comboyne, rainfor., y.pans, 19.ii.1993, DJB; 1♂, Cooranbong, Gap Ck FlR, 3–4.ii.1986, B.J. Day, DKM; 2♂♂, 1♀, Dingo Tops For. Pk, NW Wingham, rainfor., 950 m, y.pans, 19.ii.1993, DJB; 11♂♂, 4♀♀, "Lorien", 3 km N Lansdowne, nr Taree, rainfor./wet scler. for., 6.i.1988, 4–10.v.1987, 16–30.viii.1992, 20–26.ix.1992, DJB, G. Williams; 2♂♂, Lyons Ck, 8 km NW Nelligen, riv. for., y.pans, 2.i.1991, DJB; 1♂, 1♀, Mooney Mooney Ck nr Gosford, 26.i.1984, B. Duckworth, B. Day, DKM, 3.xii.1985, DJB; 2♂♂, Mt. Hyland NP, Obeloe Ck, 1030 m, 30°10'S 152°27'E, warm temp. rainfor., 25–27.i.1996, DJB; 3♂♂, 6♀♀, Mt. Kaputar NP, nr Green Ck, 950 m, y.pans, 18.xi.1990, DJB, ck at Road, 750 m, 18.xi.1990, DJB; 1♂, 2♀♀, Mt. Warning NP, 24.xi.1985, DJB & G. Cassis; 3♂♂, 2♀♀, Nadgee NP, Merrika R./Nadgee R., dry scler. for., 1.ii.1987, 13–19.ii.1987, DJB; 2♂♂, 1♀, Nadgee NP, nr Eden, 14–15.ii.1986, DJB; 7♂♂, 1♀, Royal NP, Wallumarra Tr., Bola Ck, subtrop. rainfor., y.pans, 7.xi.1993, BJS; 1♀, Royal NP, E. Waterfall, rainfor., 8.iii.1991, DJB; 4♂♂, 6♀♀, Tooloom Scrub For. Res., Legume Rd nr Urbenville, 10–11.i.1988, DJB; 5♂♂, 3♀♀, Washpool NP, Coombadjah Ck, warm temp. rainfor., 780 m, 6.xii.1992, DJB; 4♂♂, 2♀♀, Werrikimbe NP, 23.iii.1985, DJB & B. Day, Cobcroft Ck, warm temp. rainfor., 27.xii.1993, 1–5.xii.1997, DJB; 3♂♂, 3♀♀, Wilson R. Res. nr Bellangry, subtrop. for. y.pans, 5.xii.1988, DJB, 27.i.1983, DKM & K.C. Khoo; 2♀♀, National Park, 6.xii.1958, DKM; 2♂♂, Nightcap NP, Googarna Rd, NE Nimbin, 14–15.xi.1988, DJB; 4♂♂, Nightcap NP, Terania Ck, N. Lismore, 15–16.xi.1988, DJB; 2♂♂, Nightcap NP, Googarna Rd, NE Nimbin, 14–15.xi.1988, DJB; 4♂♂, Nightcap NP, Terania Ck, N. Lismore, 15–16.xi.1988, DJB (AMS); 18♂♂, 2♀♀, Barrington Tops NP, Williams R., subtrop. rainfor., 480 m, y.pans, 19–20.xii.1993, BJS, DJB (AMS, CNC); 11♂♂, 4♀♀, Blue Mtns NP, Mt. Wilson, 19.xii.1986, DKM, B.J. Day, R. de Keyzer (AMS), Waterfall Ck, 22.xi.1993, 12–13.xii.1998, BJS; 22♂♂, 4♀♀, Border Ranges NP, Brindle Ck, 800–1000 m, rainfor., y.pans, 25–26.i.1995, BJS (CNC); 5♂♂, 4♀♀, Blue Mtns NP, Wentworth Falls, Jamison Ck, 23.x.1994, 10.xi.1993, BJS (AMS, ZFMK); 2♂♂, Bruxner Pk FlR nr Coffs Harbour, Bucca Bucca Ck, subtrop. rainfor., 100 m, 1.iv.1995, BJS (ZFMK); 26♂♂, 5♀♀, Dorrigo NP, 12.x.1962, DHC (ANIC), 22–23.x.1980, subtrop. rainfor., DJB (ANIC, WOOC), Rosewood Ck, y.pans, 23.i.1995, BJS (CNC), Wonga Walk, 700 m, Crystal Shower Falls, 2.iv.1995, BJS (ZFMK); 1♂, 1♀, Fitzroy Falls, 23.i.1963, DHC (ANIC); 20♂♂, 8♀♀, Ku-ring-gal Chase NP, Gibberagong Tr., trib. Gully Ck, 20.xi.1993, BJS (ZFMK), McCarrs Ck, 28.i.1985, DJB (AMS), Cicada Ck nr Church Pt, 11.xi.1990, 28.xii.1992, DJB (AMS); 26♂♂, 12♀♀, 7 km E Robertson, Macquarie Pass NP, subtrop. rainfor., 23.xi.1993, BJS (CNC), 30.iii.1986, 27.ii.1991, DJB (AMS); 16♂♂, 16♀♀, Minnamurra Falls, 31.i.1962, 28.v.1963, 4.x.1965, DHC (ANIC), 7.i.1961, 20.x.1961, DKM (AMS), iii.1983, B.Day, K.C. Khoo (AMS); 30♂♂, 27♀♀, Royal NP, Otford, 31.xii.1962, DHC (ANIC), 6.xii.1958, 10.ii., 3.iii.1962, DKM (AMS); 15.ii.1957, W.W. Wirth (USNM); 6♂♂, 5♀♀, Royal NP, Bola Ck, subtrop. rainfor., 29.xii.1993, BJS (ZFMK), 12.ii.1985, DKM (AMS); 9♂♂, Royal NP, Couranga Tr., dry scler. for., 19.iii.1995, 23.iv.1995, 29.v.1994, BJS (CNC, ZFMK); 2♂♂, Royal NP, National Falls, 29.v.1994, BJS (ZFMK). **Queensland**: 8♂♂, 22♀♀, Bunya Mtns NP, Saddleback Ck, rainfor., 950 m, y.pans, 25–26.xi.1992, DJB, y.pans/MT, 4–6.xii.1985, DJB & G. Cassis; 1♂, 2♀♀, Horse Gully Ck, base Bunya Mtns, dry scler. 500 m, y.pans, 26.xi.1992, DJB; 10♂♂, Mt. Spurgeon, 16°26'S 145°12'E, 1250 m, wet sclero. for. & ck, y.pans, 18–19.iv.1994, DJB; 5♂♂, 1♀, Teviot Ra., Rd to Boonah below Wilsons Pk, 24.i.1995, BJS (AMS); 5♂♂, 1♀, Mt. Windsor Tableland, 16°26'S 145°12'E, 1000 m, ck, 16.iv.1994, BJS (ZFMK). **Victoria**: 13♂♂, 4♀♀, Burrowa-Pine Mtn NP, Bluff Ck Picnic A., 400 m, riverine for. y.pans, 29.xi.1994, DJB; 1♂, Errinundra Plateau, Bonang Ck, y.pans, 1.iv.1990, DJB (AMS).

Additional material (in alc.). **Australian Capital Territory**: 2♂♂, Wombat Ck, 6 km NE Piccadilly Circus, 35°19'S 148°51'E, 750 m, iv.1984, Weir, Lawrence, Johnson (ANIC).

Diagnosis. Recognized by the dark-coloured pleura, distinct iridescent pruinescence on katepisternum, distinct brush of setae at base of the male mid femur, and the tri-lobed epandrial process.

Description. Wing length 2.5–3.1 mm, similar to *C. attenuatus* except as follows:

Male. *Head*. Postocellar bristles one-third length of ocellar bristles. Antenna with length of scape less than height of eye; postpedicel apical two-thirds strongly tapered; three-segmented stylus one-fourth length of postpedicel; length of segment 8 subequal to width.

Thorax. Scutum, postnotum and pleura dark brown (pleura paler in northern populations); postpronotal lobe pale brown, with pale streak extending to base of fore coxa; scutum lacking vitta of pruinescence.

Wing (Fig. 87). Stigma faint. R_{2+3} running parallel and close to costa, smoothly arched around stigma.

Legs. Fore and mid coxae yellow, hind coxa yellowish-brown; base of femora, especially inner margin yellow, becoming dark brown towards tip. Fore femur slightly swollen, with av row of fine setae, less than half width of femur.

Mid femur slightly swollen with pv row of short, dark setae along basal two-thirds; base with long erect pv seta; base with av cluster of long stout setae, nearly equal in length to width of femur; av margin with row of short, pale setae along entire length (Fig. 99). Mid tibia slightly arched, not swollen at mid-length, with pv row of fine setae; apex with av cluster of short, erect setae; 1 erect dorsal seta near mid-length and 1 erect ad setae on basal third.

Hind femur with av row of very short setae.

Abdomen dark brown, concolorous with mesonotum; intersegmental membrane between S 6–7 often with pair of lateral patches of dark, dense microtrichia; S7 one-half longer than preceding sternite, anterolateral margin produced anteriorly, articulated with S8; T8 broad, rectangular, one-third length of sternite.

Terminalia (Figs. 120, 121). Hypandrium convex, posterior margin with flap-like extension; gonocoxal apodemes developed, slightly projected beyond anterior

margin; anterior margin of hypandrium with wing-like lateral wall upon which epandrium articulates; postgonites articulated at base of phallus, erect, slightly arched with hooked tips; phallus with pair of strongly recurved, posteriorly directed sickle-shaped processes. Epandrium lacking very long, stout setae; epandrial process forming trilobed complex: anterior lobes with rounded apex, apex of posterior lobe flattened with long dense setae; inner base of lobes with short, spine-like process; inner margin connected to internal sclerite formed from lateral expansion of bacilliform and subepandrial sclerites. Surstylus expanded apically with crown of short, stout setae; longer than epandrial process, with long marginal setulae. Cercus slender, thickly sclerotized posteriorly, with inner, apical, dense stout setae.

Female. Similar to male and female of *C. attenuatus* except as follows: apical half of postpedicel subequal to base; segment 8 of stylus nearly 4× longer than width; lacking av row of setae of fore femur; mid tibia with 2 erect ad and 1 pd seta on basal half. Posterodorsal corner of anepisternum with more expansive dark colouration. Terminalia (Fig. 122): T10 bearing biserial row of spine-like setae along posterior margin. Cercus bearing spine-like setae, with slender marginal setae. Spermathecal receptacle oval, somewhat flattened with short neck (Fig. 123).

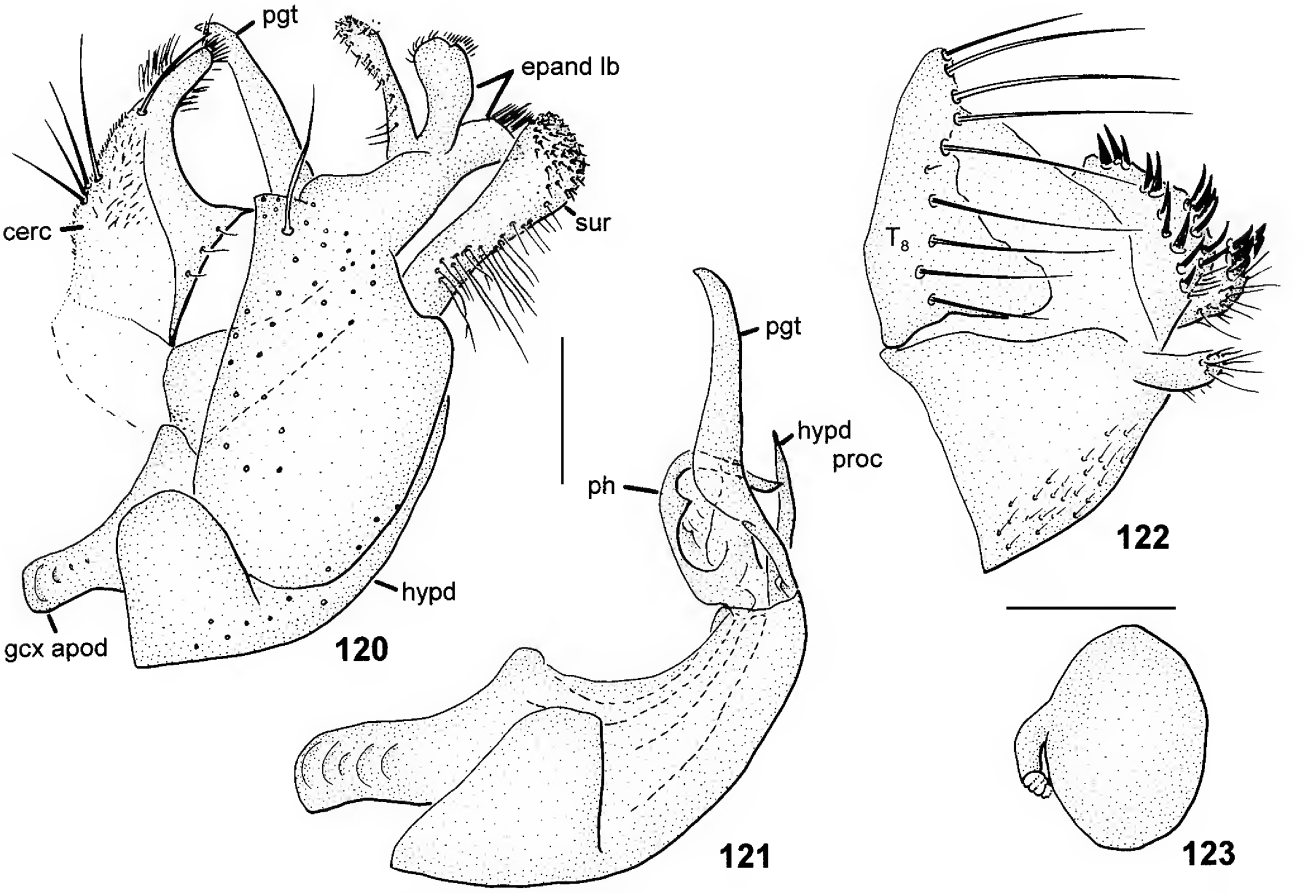
Distribution. This is the most widespread species of *Ceratomerus* in Australia, known from the Atherton Tablelands of northern Queensland to Victoria (Figs. 29, 124). The northern populations generally appear more pale in colouration.

It is also known from the upper Carnarvon Creek of Carnarvon NP (outlying western locality in southeastern Queensland, Fig. 29). The permanent waters of this montane region in southeastern Queensland are considered an oasis in an area of low and seasonal rainfall (Watson & Theischinger, 1984). Several endemic aquatic taxa are known from this region, or represent distinct populations, separate from the coastal populations.

Biology. This species is readily collected by sweeping emergent rocks in streams from a wide variety of forests, including warm and cool temperate, subtropical, and gallery rainforests. Records indicate that adults can be found year round at most localities.

In southern Queensland, this species inhabits widely disjunct watersheds. During periods of reduced rainfall, the streams occasionally are reduced to large pools, yet *C. orientalis* remains active. It is this adaptability that has enabled this species to inhabit a range of habitats, resulting in its widespread distribution.

Etymology. The specific name is from the Latin *orientalis* (of the east), referring to distribution of this species throughout the eastern margin of Australia.



Figs. 120–123. Terminalia of *Ceratomerus orientalis*, 120, male, lateral view; 121, hypandrium and phallus, lateral view; 122, female, lateral view; 123, spermatheca. Scale bars = 0.1 mm. Abbreviations: *cerc*, cercus; *epand lb*, epandrial lobe; *gcx apod*, gonocoxal apodeme; *hypd*, hypandrium; *hypd proc*, hypandrial process; *pgt*, postgonite; *ph*, phallus; *sur*, surstylus; *T*, tergite.

Zoogeography

Faunal subregion

The Ceratomerinae of Australia are presently confined to a narrow eastern zone defined by the Great Dividing Range, extending south into Tasmania. Although there are no records of this subfamily from southwestern Australia, it is clearly another example of a Bassian faunal element (Spencer, 1896), with a discontinuous northern extension along the temperate tablelands rising from the tropical and subtropical lowlands of northern Queensland (Mackerras, 1970; Nix, 1991). The distribution of Australian Ceratomerinae could also be termed an element of the Kosciuskan subregion as reviewed by Heatwole (1987) or what Bickel (1994) termed the "Eastern Forest". However, these two subregions do not include Tasmania. Other Empidoidea with a similar distribution to that of Australian Ceratomerinae, include the Clinocerinae and *Hydropeza* (Sinclair, 1999, 2000b). While *Apterodromia* Oldroyd has a similar distribution, it is also known from southwestern Australia (Sinclair & Cumming, 2000).

Regional patterns

The diversity of Ceratomerinae in Australia is greatest in the southeast, as for many aquatic groups. Although the Border Ranges of northern New South Wales include four species, all represent widespread taxa and no endemic species have been found in this region.

Northern Queensland-Tasmania disjuncts. In the *C. campbelli* group, there is an example of a widely disjunct sister-species pairing. *Ceratomerus campbelli* (Tasmania) is clearly most closely related to *C. athertonius* from the Northern Tablelands on the basis of similar secondary sexual modifications of the male wing. A similar disjunct sister-species pair is known also in the aquatic genus *Clinocera* (Sinclair, 2000b).

Areas of endemism. Five of seven species of *Ceratomerus* are known only from Tasmania (71% endemism). In other aquatic taxa, high Tasmanian species-level endemism is also reported in Blephariceridae (100%), Plecoptera (nr 90%), and Trichoptera (74%) (Zwick, 1977; Hynes & Hynes, 1982; Williams & Campbell, 1987; Neboiss, 1991). In Odonata, two endemic cold-water genera are known, suggesting long isolation of stream faunas (Watson & O'Farrell, 1991). Although Tasmania was connected to the mainland during the Pleistocene, the land bridges were primarily low plains, and mostly unfavourable to cool-adapted species (Hynes & Hynes, 1982; White, 1994). Among other Empidoidea, Tasmanian endemics are also known in terrestrial *Apterodromia* (100%) and the aquatic genera *Hydropeza* (100%) and *Clinocera* (33%) (Sinclair & Cumming, 2000; Sinclair, 2000b). Bickel (1998) estimates that there may be more than 100 Tasmanian species of Hilarini, including an endemic genus, *Cunomyia* Bickel.

The remarkable diversity of *Ceratomerus* in Barrington Tops National Park is a reflection of the range in altitude and resulting floral changes found there. Nine species are reported with two species currently endemic, or known only from the Park. *Ceratomerus barringtonensis* is known from both 480 m and 1280 m, while *C. oreas* is known only from the *Nothofagus* region above 1200 m. The southern species, *C. maculatus* and its northern sister species, *C. falcatus* are both found here, but the former is recorded only from 1200 m and the latter from the subtropical area at 480 m. The widespread *C. orientalis* is found from 380 to above 1200 m and the southern species, *C. albistylus* is found only at higher elevations.

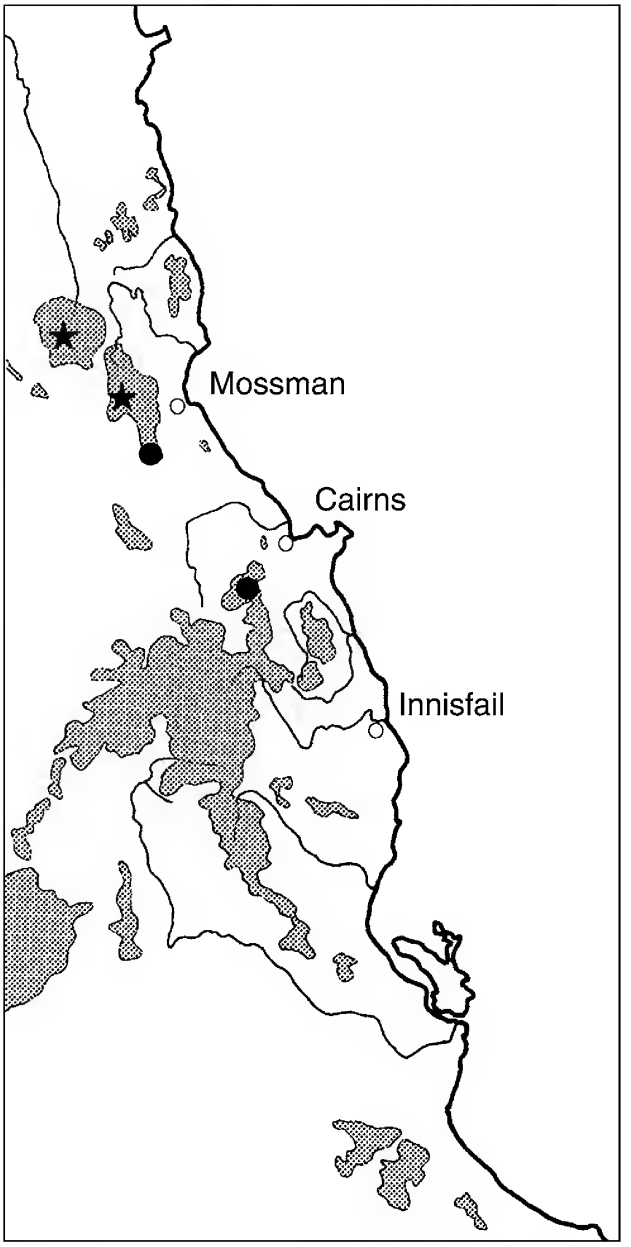


Fig. 124. Known distribution of species of *Ceratomerus* (northern Queensland). *Ceratomerus athertonius* ●, *C. orientalis* ★. Shaded areas indicate land above 700 m in altitude.

Widespread species patterns. *Ceratomerus orientalis* is the most widespread species, ranging from northern Victoria to southern Queensland (including Carnarvon NP), with an isolated population in the Tablelands west of Cairns. Most widespread species such as *C. orientalis* are found in both remnant and gallery rainforests. The latter are surrounded by sclerophyll forests (e.g., Royal National Park south of Sydney). In contrast, although *C. albistylus* is the second most widespread species ranging from Tasmania to New England National Park, it is recorded mostly from cool, wet rainforests. All species of *Ceratomerus* with very restricted ranges are confined to remnant rainforests and have not been recorded from gallery rainforests.

Two widespread species in the southeast (*C. albistylus* and *C. maculatus*) are common at both higher and lower altitudes as far north as Sydney. While populations north of Sydney are confined to areas above 1000 m. In addition, *C. lobatus* appears to be an example of a Bassian element with coastal populations present primarily in the cooler months. This pattern was discussed by Mackerras (1950).

Norfolk Island. Norfolk Is. is volcanic in origin, located in the southwestern Pacific, between New Caledonia and New Zealand and some 1400 km east of the coast of Australia (Rentz, 1989). There are three main islands in the Norfolk group, of which the ecologically devastated Philip Is. is 6 km south of Norfolk. It is estimated that the islands are 2.8–3 million years old and the biota could not have existed until after the late Pliocene (Rentz, 1989).

The present fauna arrived via transoceanic dispersal during the past two million years. During lower sea-level periods associated with Pleistocene glaciation (lowered approx. 100 m), the islands would have still been as isolated as today, although several small stepping stone islands probably existed that aided dispersal (Holloway, 1977; Rentz, 1989).

There has been no detailed study of the empidoids of Norfolk Is. Bickel (1994, 1996) reported three non-endemic species of Sciapodinae (Dolichopodidae) from Norfolk Is., of which two were probably accidentally introduced. All species also occur in Australia. The single species of *Ceratomerus* recorded from Philip Is. is clearly of the *C. ordinatus* group and thus of Australian origin. This species group is not known from New Zealand and no ceratomerines have yet been discovered from New Caledonia (Sinclair, unpubl. data) and the highlands of New Guinea. Additional material, especially males are required to determine the status of this species from Philip Is.

Affinities

The Southern Hemisphere distribution of the Ceratomerinae has long been noted, with the first species described from the early decades of the twentieth century. Paramonov (1959) and Hennig (1960) included the Ceratomerinae as possible examples of Trans-Antarctic (Southern) or Gondwanan elements, but lacked knowledge of relationships for discussion of this geographic distribution.

The two major Australian species-groups display contrasting zoogeographic relationships. The *C. ordinatus* group share apparent derived characters with several species from New Zealand and South America, while the *C. campbelli* group are clearly most closely related to the *C. paradoxus* group of southern South America (see "Phylogenetic affinities" for further details). Together with remaining Australian species (*C. inflexus* group and unassigned species), the latter two species groups constitute the sister group to a lineage of closely related New Zealand species.

Phylogenetic affinities

As stated above, the Australian species of *Ceratomerus* can be divided clearly into two monophyletic units, but they are not monophyletic as an entire group. The monophyly of the *C. ordinatus* group in comparison to other Australian species is supported on the basis of the following synapomorphies: lengthened pedicel (second antennal segment), stigma absent, long postocular bristles overlapping eye, and third dorsocentral bristle shorter than others. On the basis of an unpublished preliminary cladistic analysis (Sinclair, 1998), the *C. ordinatus* group is possibly most closely related to several New Zealand and Ecuadoran (high altitude) species. Within this species-group, *C. maculatus* appears to be the sister species of *C. falcatus* on the basis of an auxiliary crossvein and sickle-shaped postgonites (Figs. 77, 80, 83, 103).

The monophyly of all remaining Australian species is supported on the following synapomorphies: pair of long, bristle-like antepronotal setae, one notopleural bristle, acrostichal setulae directed anteriorly (except *C. albistylus*), prescutellar pair of dorsocentral bristles shorter than others, stigma positioned at apex of cell r_1 and proximal end truncate, and single basoventral seta on hind first tarsomere. Within this group, the *C. campbelli* group alone is most closely related to the *C. paradoxus* group from Chile (Sinclair, 1998). This relationship is supported on the basis of the following synapomorphies: inner apical margin of the male fore coxa concave, not evenly tapered and greatly distorted male midlegs bearing tubercles, extra lobes, and modified setae. Within the *C. campbelli* group, *C. athertonius* and *C. campbelli* are sister species (see under Zoogeography) on the basis of long spatulate setae at the basal margin of the male wing (Fig. 11). The other two species of this group, *C. barringtonensis* and *C. victoriae* also form a sister species pairing on the basis of stout setae on the margin of the anal lobe of the male wing (Figs. 12, 14) and the large thumb-like ventral lobe of the male mid femur (Figs. 3, 7).

In the *C. inflexus* group, *C. macalpinei* and *C. malleolus* are very closely related sister species on the basis of male terminalia, especially the form the cercus, proctiger lobe, and surstylus (Figs. 66, 69). Also in this group, the male cercus of *C. bulbosus, C. inflexus* and *C. oreas* is unique in its shape and setation (Figs. 46, 63, 72). These five species, plus *C. bickeli* are closely related on the basis of spherical epandrial lamellae, which may often be greatly inflated more broadly than the width of the abdomen.

Further refinement of the relationships of Australian species of *Ceratomerus* could not be resolved through traditional morphological methods. It is possible that molecular phylogenetic techniques may improve the resolution and certainly could be used to test the relationships proposed in this study.

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Groenlandaspidid Placoderm Fishes from the Late Devonian of North America

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ABSTRACT. Two new taxa of groenlandaspidid fish (Placodermi: Arthrodira) from non-marine deposits of the Catskill Formation (Upper Devonian) at Red Hill, Clinton County, Pennsylvania, USA, are the first to be described from North America outside of Greenland. *Groenlandaspis pennsylvanica* n.sp. is known only from isolated trunk elements that are quite similar to *Groenlandaspis antarctica* Ritchie, 1975. *Groenlandaspis pennsylvanica* n.sp. is characterized by distinct features of the median dorsal (MD), posterior dorsolateral (PDL), and anterior dorsolateral (ADL) plates. *Turrisaspis elektor* n.gen. and n.sp. is a smaller form with a high median dorsal plate (MD) and tall, narrow elements of the dorsolateral trunk shield, particularly the PDL, giving this taxon a distinctively short, high trunk shield. The head shield of *Turrisaspis elektor* has a divided pineal plate and the postmarginal plate makes contact with the postorbital plate, excluding the marginal plate from the lateral margin of the head shield. *Groenlandaspis pennsylvanica* n.sp. is a rare faunal component at the Red Hill site whereas *Turrisaspis elektor* is very common. The large sample size of *Turrisaspis elektor* provides a glimpse at ontogenetic and individual variation within this taxon.

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Groenlandaspidid placoderms have been reported from strata as old as Early Devonian, but the diversity is particularly well documented during the Late Devonian. The earliest known member of the family is *Tiaraspis subtilis* from the Early Devonian of Germany (Gross, 1933, 1962; Schultze, 1984). Other groenlandaspidids from the Euramerican Province are *Groenlandaspis mirabilis* from the Famennian of eastern Greenland (Heintz, 1932), and *Groenlandaspis disjectus* from Ireland (Woodward, 1891; Ritchie, 1975). Gross (1965) discusses isolated groenlandaspidid median dorsal elements from the Famennian of Belgium. The Gondwanan Province has produced *Groenlandaspis theroni* from the Givetian of South Africa (Chaloner *et al.*, 1980; Anderson *et al.*, 1999), *Groenlandaspis antarctica* and *Boomeraspis goujeti* from the late Givetian to early Frasnian Aztec Siltstone in Victoria Land, Antarctica (Ritchie, 1975; Long, 1995), *Groenlandaspis seni* from the ?Frasnian of Turkey (Janvier & Ritchie, 1977), and *Groenlandaspis riniensis* and *Africanaspis doryssa* from the Famennian of South Africa (Long *et al.*, 1997). Janvier & Ritchie (1977, fig. 1E) and Blieck *et al.* (1980) discuss groenlandaspidid material from the Eifelian of Iran. Janvier

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Table 1. Red Hill flora and fauna.

- Kingdom Animalia
  - Subphylum Vertebrata
    - Class Placodermi
      - Order Phyllolepida
        - Family Phyllolepididae
          - *Phyllolepis* sp.
      - Order Arthrodira
        - Family Groenlandaspididae
          - *Groenlandaspis pennsylvanica* n.sp.
          - *Turrisaspis elektor* n.gen. and n.sp.
    - Class *incertae sedis* Acanthodii
      - Order Climatiiformes
        - Family Gyracanthidae
          - *Gyracanthus* cf. *G. sherwoodi* Newberry
    - Class Chondrichthyes
      - Order Ctenacanthiformes
        - Family Ctenacanthidae
          - *Ctenacanthus* sp.
      - Order indet.
        - *Ageleodus pectinatus* (Agassiz)
    - Class Osteichthyes
      - Subclass Actinopterygii
        - Order Palaeonisciformes
          - *Limnomis delaneyi* Daeschler
      - Subclass Sarcopterygii
        - Order Dipnoi
          - Family indet.
        - Order Crossopterygii
          - Family Megalichthyidae
            - gen. and sp. indet.
          - Family Tristichopteridae
            - *Hyneria lindae* Thomson
          - Family Rhizodontidae
            - cf. *Sauripterus* sp.
    - Class Amphibia
      - Order Ichthyostegalia
        - Family *incertae sedis*
          - *Hynerpeton bassetti* Daeschler *et al.*
          - *Densignathus rowei* Daeschler
  - Subphylum Chelicerata
    - Class Arachnida
      - Order Trigonotarbida
        - Family Palaeocharinidae
          - *Gigantocharinus szatmaryi* Shear
  - Subphylum Myriapoda
    - Class Diplopoda
      - Order Archipolypoda
- Kingdom Plantae
  - Division Tracheophyta
    - Class Zosterophyllopsida
      - Order Barinophytales
        - *Barinophyton* spp.
    - Class Lycopsida
      - Order Isoetales
        - cf. *Lepidodendropsis* sp.
    - Class Filicopsida
      - Order Zygopteridales
        - *Rhacophyton* sp.
      - Order Stauropteridales
        - *Gillespiea* sp.
    - Class Progymnospermopsida
      - Order Archaeopteridales
        - *Archaeopteris* spp.
    - Class Gymnospermopsida
      - Order Pteridospermales
        - cf. *Aglosperma* sp.

& Villarroel (2000) report possible groenlandaspidid remains from the Frasnian of Columbia. Ritchie (1974, 1975), Young (1999), and others mention currently undescribed forms of *Groenlandaspis* from Frasnian and Famennian localities in New South Wales, Australia. Janvier *et al.* (1984) report *Groenlandaspis* from the ?Tournaisian of southeast Turkey. This paper describes two new taxa of Late Devonian (late Famennian) groenlandaspidids from non-marine beds at the Red Hill site in north-central Pennsylvania, USA. These are the first reported North American groenlandaspidids outside of Greenland and they reinforce the cosmopolitan distribution of the group in the Late Devonian.

The Red Hill fossil site is located in central Clinton County, Pennsylvania, USA (Fig. 1). The locality is a one-kilometre-long road cut through the upper part of the Duncannon Member of the Catskill Formation. The Duncannon Member is approximately 250 meters thick in this part of north-central Pennsylvania and is regarded as non-marine in origin, the deposits of meandering fluvial systems on a broad alluvial plain (Berg *et al.*, 1983; Sevon, 1985; Woodrow *et al.*, 1995). The Red Hill road cut exposes a 30-meter section of the Duncannon Member and within that sequence the fossiliferous zone producing all of the vertebrate material in this report is about two meters thick (the fossiliferous zone is marked with asterisk in Fig. 1). Since 1993, the site has produced a diverse fauna and flora (Table 1), providing a snapshot of a Late Devonian freshwater / terrestrial assemblage.

The environments of deposition for the fossiliferous zone at Red Hill are interpreted as shallow channel margin facies and overbank pond facies (Daeschler & Cressler, 1999). Groenlandaspidids are one of the most abundant macro-vertebrates at the Red Hill site. The two taxa presented here occur together in all lithofacies within the fossiliferous zone. Although disarticulated groenlandaspidid material is common throughout the fossiliferous zone, one bedding plane within the channel margin facies contained an area of several square meters with abundant articulated, although crushed, remains. This layer preserves *Turrisaspis elektor* n.gen. and n.sp. of varied sizes in a density of approximately 20 individuals per square meter. The horizon also preserves articulated, although less abundant material of an unidentified acanthodian and *Limnomis delaneyi*, the only actinopterygian known from the Red Hill site (Daeschler, 2000b). This horizon may represent a mass mortality event within the channel margin facies, perhaps the result of stranding in an ephemeral pool as water levels fluctuated.

The Catskill Formation in Pennsylvania has a long history of vertebrate palaeontological studies prior to the recent work at Red Hill. In 1843, James Hall described a pectoral fin and scales of a large rhizodont sarcopterygian, *Sauripterus taylori*, from undifferentiated Catskill Formation in southern Tioga County. This fin has played prominently in discussions of the origin of the tetrapod limb, although no additional material of *Sauripterus* was found in the Catskill Formation until 1995 when another pectoral fin was found (Daeschler & Shubin, 1998). The porolepiform sarcopterygian *Holoptychius americanus* Leidy, 1856 was described from the Catskill Formation in Tioga County and isolated scales of *Holoptychius* sp. are commonly encountered at most fossiliferous sites. Newberry (1889) described the phyllolepid placoderm,

Phyllolepis delicatula, from the Catskill Formation near Leroy, Bradford County. This genus is also found at the Red Hill site and is presently under study. The antiarch placoderm *Bothriolepis* is the most common taxon found in the Catskill Formation. *Bothriolepis nitida* (Leidy, 1856) and *Bothriolepis minor* Newberry 1889 were each described from the Catskill Formation in Tioga County. Weems *et al.* (1981) described *Bothriolepis virginiensis* from Catskill equivalent strata in Virginia. Thomson & Thomas (2001) and Young (1988, fig. 65H) provide illustrations of *Bothriolepis* material from the Catskill Formation in Pennsylvania. In the 1960s and 1970s Keith S. Thomson and students from Yale University collected at various sites in the Catskill Formation and described the large tristichopterid sarcopterygian, *Hyneria lindae* Thomson, 1968 and the megalichthyid sarcopterygian, *Sterropterygion brandei* Thomson, 1972 from Clinton and Lycoming Counties, respectively. Recent work has also reported on material of the acanthodian *Gyracanthus* sp. from Sullivan County (Sullivan *et al.*, 1999). Recent palynomorph biostratigraphic studies of some fossil sites within the Catskill Formation in Clinton and Lycoming Counties indicate a Famennian age for the recently worked sites (Traverse, pers. comm.). Precise stratigraphic control for earlier sites is not available.

Red Hill in Clinton County has produced the unique faunal assemblage presented in Table 1. (Daeschler *et al.*, 1994; Daeschler, 1998; Cressler, 1999; Daeschler, 2000a,b; Shear, 2000; Davis *et al.*, 2001; Downs & Daeschler, 2001). Red Hill is the only site in the Catskill Formation that has yielded groenlandaspidid material. The Red Hill fauna stands in sharp contrast to the more commonly encountered *Bothriolepis* and *Holoptychius*-dominated fauna of the Sherman Creek Member of the Catskill Formation. Neither *Bothriolepis* nor *Holoptychius* is found at Red Hill although Daeschler *et al.* (1994) erroneously listed *Bothriolepis* from the Red Hill site based on fragmentary, ornamented plates that have now been re-identified as groenlandaspidid. These distinct ichthyofaunas within the laterally-equivalent facies of the Catskill Formation represent different sedimentological and palaeoecological settings within the Catskill Delta complex (Daeschler, 1998).

Methods and materials. Most specimens were prepared mechanically with a sharpened carbide rod. A few specimens in which the bone was crushed or poorly preserved were placed in a 10 percent HCl solution for 24 to 48 hours to dissolve the bone and leave a detailed mold of the specimen in fine sandstone matrix. The acid-etched mold was covered with several thin layers of latex, allowed to dry thoroughly, and pulled off to obtain a latex peel. Most specimens and all latex peels were coated with ammonium chloride prior to imaging. All specimen images were captured digitally with a Kodak Digital Camera System 460.

Measurements were made on isolated elements and head shields that were complete enough to get accurate data using callipers. Height, length and width measurements were made following the methods illustrated in Figs. 10 and 12.

Abbreviations used in the text and figures are as follows. ADL, anterior dorsolateral plate; AL, anterior lateral plate; AMV, anterior median ventral plate; APi, anterior pineal plate; AVL, anterior ventrolateral plate; Ce, central plate; IL, interolateral plate; M, marginal plate; MD, median

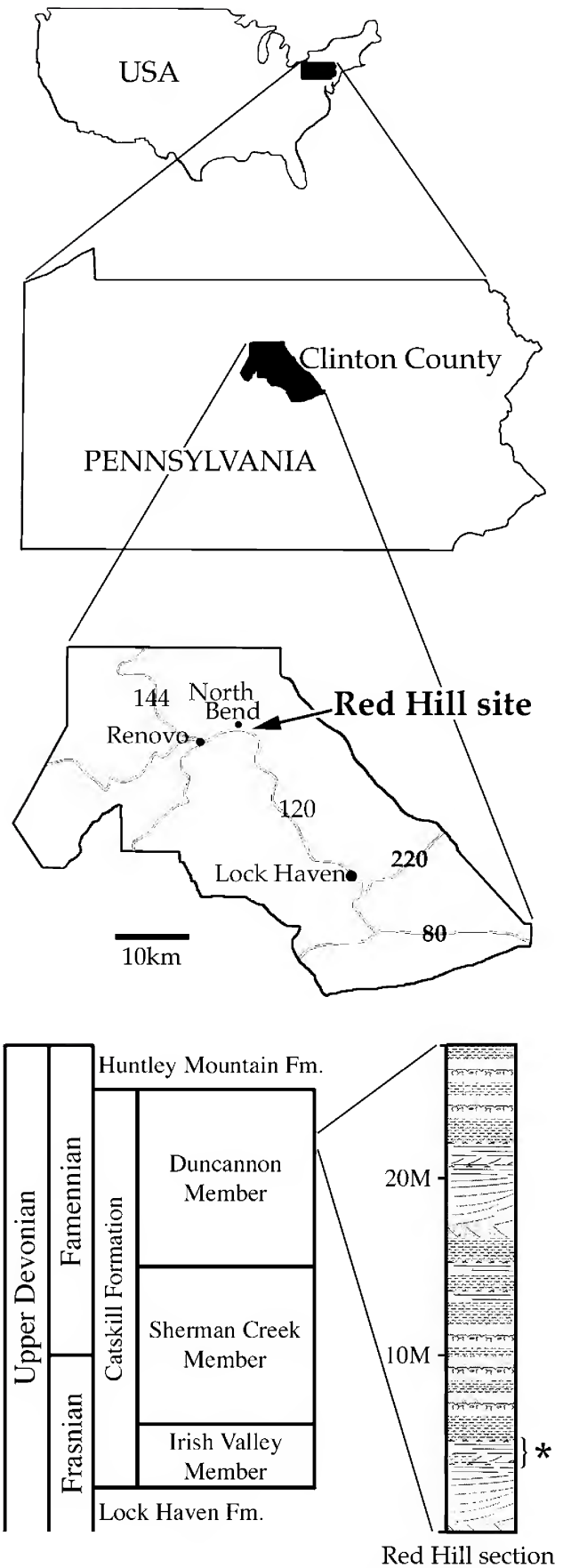


Fig. 1. Location and stratigraphic framework of the Red Hill site, Clinton County, Pennsylvania, United States of America. Two-meter-thick fossiliferous zone marked with an asterisk.

dorsal plate; Nu, nuchal plate; PDL, posterior dorsolateral plate; Pi, pineal plate; PL, posterior lateral plate; PM, postmarginal plate; PMV, posterior median ventral plate; PNu, paranuchal plate; PPi, posterior pineal plate; PrO, preorbital plate; Psp, parasphenoid; PtO, postorbital plate; PVL, posterior ventrolateral plate; R, rostral plate; Sgn, supragnathal; SP, spinal plate. Museum acronym: ANSP, The Academy of Natural Sciences of Philadelphia.

Systematic palaeontology

Class Placodermi McCoy, 1848
Order Arthrodira Woodward, 1891
Suborder Phlyctaenioidei Miles, 1973
Family Groenlandaspididae Obruchev, 1964
Genus *Groenlandaspis* Heintz, 1932

Type species. *Groenlandaspis mirabilis* Heintz 1932; Late Devonian, East Greenland.

Groenlandaspis pennsylvanica n.sp.

Figs. 2–4

Holotype (Fig. 2B). ANSP 20755, median dorsal plate (MD) in right lateral view and partially exposed in left lateral view. Complete except for missing tip of the anteroventral projection. Ventral margin slightly crushed.

Other material. All of the material of this species consists of isolated trunk plates: 9 ALs (3 complete and 6 partial); 1 ADL (complete); 10 PDLs (5 complete and 5 partial); 4 MDs (2 complete and 2 partial); 1 AVL (partial); 1 PVL (partial). Specimen catalogue numbers and the measurements of complete elements are listed in Appendix 1.

Locality and horizon. USA, Pennsylvania, Clinton County, Red Hill site, north side of Route 120, 1 km east of the village of North Bend (41°20.633'N 77°40.814'W) (Fig. 1). Catskill Formation, Duncannon Member.

Age. Late Devonian, late Famennian Stage (Fa2c substage); *Grandispora cornata* / *Rugispora flexuosa* palynomorph zone (Traverse, in press).

Etymology. Named for the State of Pennsylvania where this taxon was discovered and studied.

Diagnosis. The MD has a low profile (average H/L = 0.48) with ornament of coarse tubercles along the anterodorsal margin and covering the lateral surface of the posteroventral region with the largest tubercles on the posterodorsal margin. Ornament of fine ridges on the MD radiate from apex to the ventral margin. The dorsal margin of the ADL is steeply inclined with a narrow anterodorsal overlap zone for the MD. The lateral surface of the PDL is ornamented with fine tubercles that form ridges radiating from the bend in the sensory canal.

Remarks. The specimens referred to *G. pennsylvanica* occur as isolated plates within the 2-meter-thick fossiliferous zone at Red Hill. Although no articulated trunk armour has been discovered, the material is believed to be from a single taxon because the elements "fit together" both in terms of size and the shapes of plate margins and overlap zones. When compared to other groenlandaspidid material from the same fossiliferous zone at Red Hill, the *G. pennsylvanica* specimens are significantly larger and the trunk shield shape is much lower and longer. There is no overlap in the size or shape characteristics of most trunk elements between the two groenlandaspidid taxa at Red Hill.

Description

ADL (anterior dorsolateral plate) (Figs. 2C, 4C). The ADL is known from a single specimen, ANSP 20743 (Fig. 2C), which is exposed in lateral view. This specimen is missing narrow parts of the caudal and ventral margins, although the natural mold of the overall shape of the element is preserved in the matrix. The dorsal and anteroventral margins are steeply inclined giving the entire element a tall, rhomboidal shape. It is difficult to quantify the shape of the ADL in a way that allows comparison to other taxa but for this paper we have derived a measure of the angle of the dorsal margin relative to the dorsolateral sensory canal on the ADL (see Fig. 2C'). On ANSP 20743, the angle formed by lines tracing the dorsal margin and the general trend of the dorsolateral sensory canal is 55°. The overlap zone for the median dorsal plate on the dorsal margin of the ADL is narrow along the anterodorsal margin and wider posteriorly. The ornament on the ADL consists of fine tubercles distributed evenly across the dermal surface. Height and length measurements for the single ADL are presented in Appendix 1.

PDL (posterior dorsolateral plate) (Figs. 2D,E; 4B). The PDL is known from ten specimens (5 complete and 5 partial). The overlap area for the MD reaches the caudal margin at the tip of a pronounced posterodorsal projection. The dorsolateral sensory canal comes to a rounded apex slightly caudal to the centre of the element where its path bends at 90°. The ornamentation on the lateral surface of the PDL consists of rows of fine tubercles radiating from the bend in the sensory canal toward the edges. The medial surface of the PDL (Fig. 2E) has a central, thickened zone extending from the centre of the ventral margin to the symphysial area where the left and right sides of the trunk shield met beneath the median dorsal plate. The angle formed by this symphysial surface and the body of the PDL is about 35° suggesting that the two sides of the trunk diverged at an angle of 70° from beneath the MD (Fig. 3). The height of the symphysial surface is about 30% of the total height of the PDL. Height and length measurements for the five complete PDL plates are presented in Appendix 1.

AL (anterior lateral plate) (Figs. 2F,G; 4D). The AL is known from nine specimens (4 complete and 5 partial). The shape is rhomboidal with the length about twice the height. The caudal margin is concave, and the cranial margin slopes to a point ventrally. The lateral surface has a raised crest that slopes upward from the anteroventral tip and bifurcates slightly cranial to the centre of the element, forming two raised crests that diverge toward the caudal margin (Fig. 2F). The ornamentation on the lateral surface consists of fine tubercles randomly distributed and fine ridges near the ventral margin. The medial surface is smooth with contours mimicking the lateral surface (Fig. 2G). Height and length measurements for the three complete AL

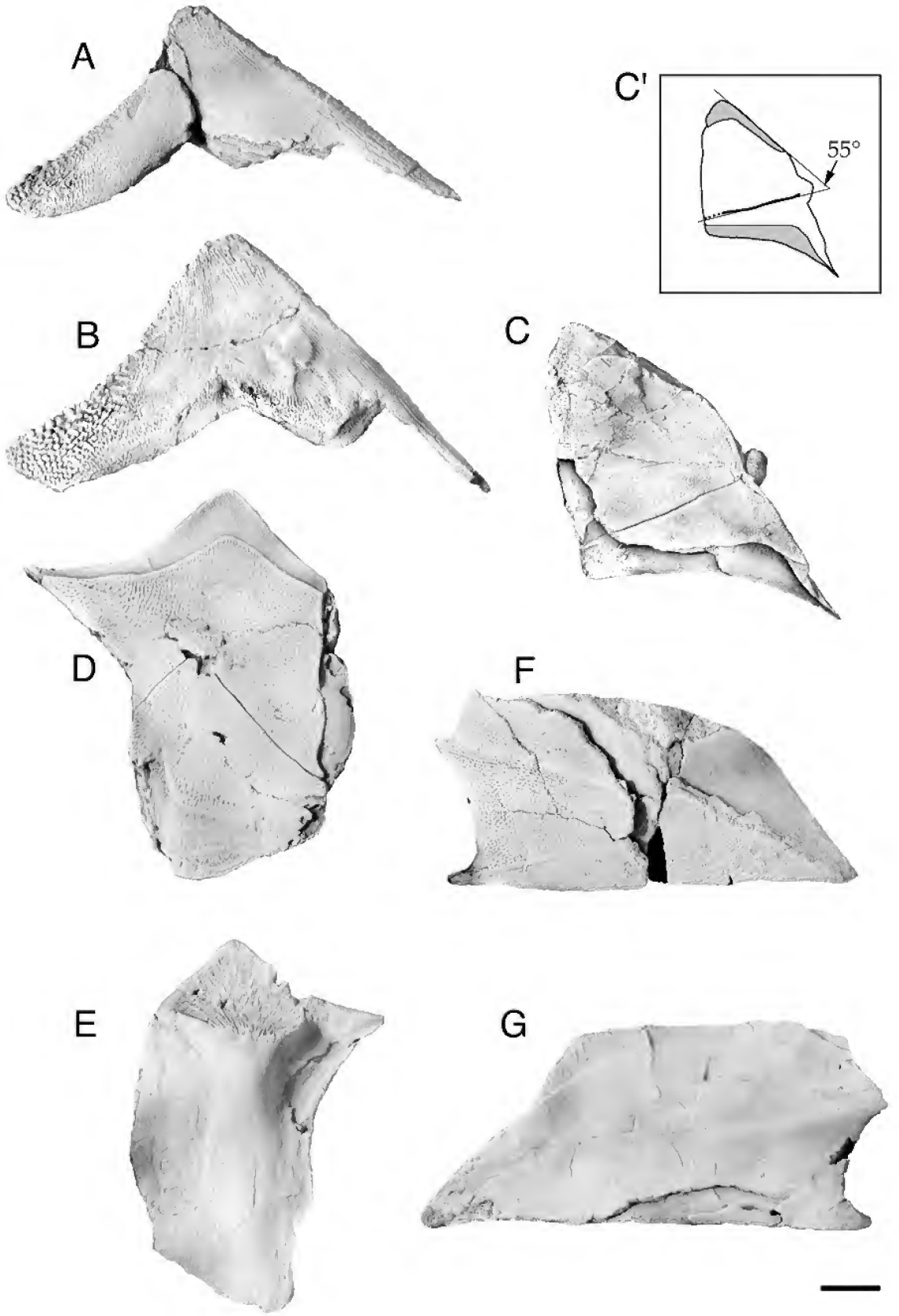


Fig. 2. Trunk plates of *Groenlandaspis pennsylvanica*. Median dorsal plates (MD): *A*, ANSP 20753; *B*, ANSP 20755. Anterior dorsolateral plate (ADL): *C*, ANSP 20743 lateral aspect; *C'*, method for measuring the angle of the dorsal margin of the ADL. Posterior dorsolateral plates (PDL): *D*, ANSP 20725, lateral aspect; *E*, ANSP 20700, medial aspect. Anterior lateral plates (AL): *F*, ANSP 20940, lateral aspect; *G*, ANSP 20727, medial aspect. All specimens whitened with ammonium chloride. Scale bar = 1 cm.

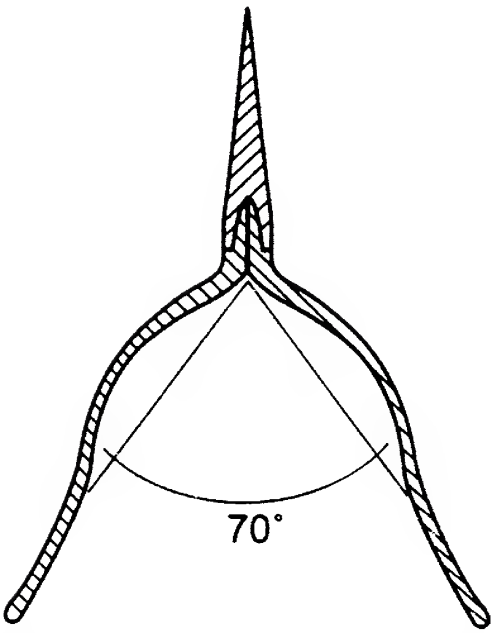


Fig. 3. Schematic cross-section of the dorsolateral and dorsal trunk shield of *Groenlandaspis pennsylvanica* determined by the angle of internal symphysis of the PDL.

plates are presented in Appendix 1.

MD (median dorsal plate) (Figs. 2A,B; 4A). The median dorsal plate of *G. pennsylvanica* is known from five specimens (3 complete and 2 partial). The general shape of the MD is long and low with a height to length ratio (using the measuring method shown in Fig. 10) of about 0.5. The blunt apex of the MD makes an 80° to 90° angle midway along the total length of the element. The anteroventral projection of the MD, where it overlaps the ADL, is long and narrow. Ornamentation of coarse tubercles is found along the anterodorsal margin and covers the posteroventral area of the element, with the largest elements of ornament along the posterodorsal margin. Ornamentation of fine striations radiating from the apex to the ventral margin covers the rest of the MD. Height and length measurements for the 3 complete MD plates are presented in Appendix 1.

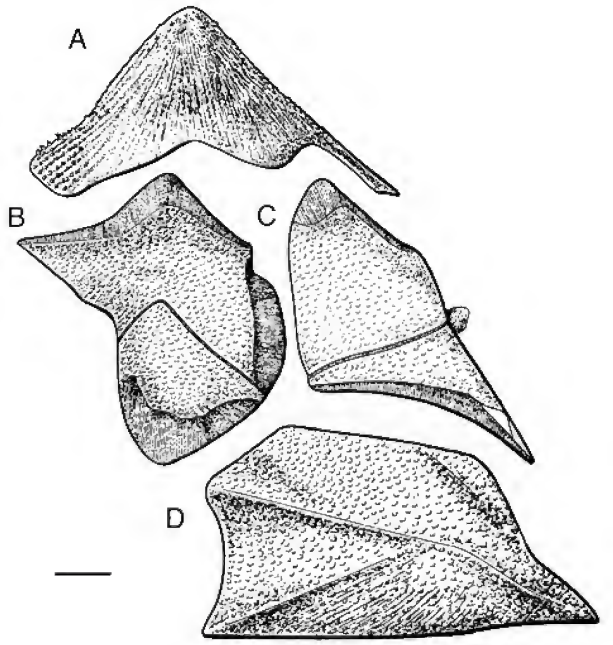


Fig. 4. Reconstructed lateral and median dorsal plates of *Groenlandaspis pennsylvanica* (PL not known). *A*, MD; *B*, PDL; *C*, ADL; *D*, AL. Scale bar = 1 cm.

Ventral Trunk. It is worth mentioning two incomplete ventral trunk elements here because they are the only examples of such material encountered. These specimens are judged to belong to *G. pennsylvanica* because they are significantly larger and morphologically distinct from material described later in this paper as *Turrisaspis elektor*. ANSP 21324 is a partial left AVL (anterior ventrolateral plate) with a length of at least 60 mm and a width of 38mm. The dermal surface is smooth except for a few scattered small tubercles near the centre of the plate, fine ridges along the posterolateral margin, and finely-reticulate ornament in the V-shaped depression in the posterolateral quadrant. ANSP 21288 is a partial right PVL (posterior ventrolateral plate) with a total length of at least 53 mm and a width of at least 42mm. Along the posterior half of the medial margin is a distinct overlap zone for the left PVL. Ornamentation of tubercles is well developed posteriorly, with the largest tubercles along the ridge where the lateral flange of the PVL angles dorsally. The tubercular ornament thins anteriorly to a smooth surface with only scattered tubercles. The aforementioned specimens, ANSP 21324 (AVL) and ANSP 21288 (PVL), occur in close proximity (3 mm) to one another on the same matrix block, but their association is uncertain.

Comparison to other species of *Groenlandaspis*

The elements of the trunk shield of *Groenlandaspis pennsylvanica* (Figs. 2, 4) are similar to those of the well-documented taxon *Groenlandaspis antarctica* (Ritchie, 1975, fig. 2; Denison, 1978, fig. 44A–C). There are, however, some morphological features of *Groenlandaspis pennsylvanica* that justify its status as a distinct species. The ADL of *Groenlandaspis pennsylvanica* has a more narrow and tall shape with a steeper dorsal margin than *Groenlandaspis antarctica*. The angle of the dorsal margin of *Groenlandaspis antarctica*, measured from published illustrations with the method shown in Fig. 2C', is 42°, as opposed to 55° in *Groenlandaspis pennsylvanica*. This comparison is only tentative because of very limited sample size (n=1) for each taxon. The ornament on the lateral trunk elements of *Groenlandaspis pennsylvanica* consists of fine tubercles that are evenly distributed or in some areas, particularly the PDL, arranged in rows, forming fine ridges. The MD of *Groenlandaspis pennsylvanica* has the same general shape as *Groenlandaspis antarctica* but details of the ornament such as fine ridges radiating from the apex, and a narrow anteroventral projection, are distinct. Aside from the morphological differences, the early Frasnian age and Gondwanan occurrence of *Groenlandaspis antarctica* also suggest that the two taxa are not conspecific.

Comparisons to the Late Devonian Euramerican forms *G. disjectus* and *G. mirabilis* are confounded by the incomplete nature of those taxa. The PDL is known from many groenlandaspidids, however, and can provide informative comparisons among most of the groenlandaspidid taxa. Figure 5 provides a comparison of the size

and shape of groenlandaspidid PDLs re-drawn from published accounts. As mentioned above, the PDL of *G. pennsylvanica* is very similar in shape to *G. antarctica* (Fig. 5B), but distinctive ornament characterizes each. The PDL of *G. disjectus* (Fig. 5C) and *G. mirabilis* (Fig. 5D) have different shapes than *G. pennsylvanica* (Fig. 5A), particularly in the dorsal margin and posterodorsal projection. The PDLs of other groenlandaspidid taxa (Fig. 5E–J) are very different in shape from *G. pennsylvanica*. Such a comparison does not illustrate the variation found within any of the taxa.

Groenlandaspis pennsylvanica is rare at the Red Hill site, known only from the aforementioned 27 isolated trunk plates. Smaller groenlandaspidid material with morphologies distinct from *G. pennsylvanica* is found in the same 2-meter-thick fossiliferous zone and is much more abundant. This smaller material is described below from 81 complete isolated trunk plates, 10 measurable head shields, and five partially articulated ventral trunk shields.

Turrisaspis n.gen.

Type species. *Turrisaspis elektor* n.sp., monotypic.

Etymology. From the Latin for spire, "turris", and Greek for shield, "aspis".

Diagnosis. As for species, by monotypy.

Turrisaspis elektor n.sp.

Figs. 6–9, 11

Holotype (Fig. 6). ANSP 20961A, articulated specimen on matrix block with right lateral view of trunk shield and dorsolateral view of head shield (Fig. 6A). The counterpart (ANSP 20961B) was etched in 10% hydrochloric acid to make a clean external mold of the specimen. Figure 6B is a whitened latex peel of the counterpart block. The counterpart lacks areas with impressions of the AL and SP. Figure 6C is a labelled drawing of ANSP 20961A/B showing plate boundaries and sensory canals.

Other material. *Turrisaspis elektor* is known from the following 81 isolated, measurable elements: MD, 29; PDL, 5; ADL, 7; AL, 11; PL, 6; AVL, 12; PMV, 7; PVL, 1; SP, 3. Additionally there are 10 measurable head shields and 5 articulated ventral trunk shields. See Figs. 10 and 12 for methods used to take measurements and Appendix 2 for specimen catalogue numbers and measurements.

Locality and horizon. USA, Pennsylvania, Clinton County, Red Hill site, north side of Route 120, 1 km east of the village of North Bend (41°20.633'N 77°40.814'W) (Fig. 1). Catskill Formation, Duncannon Member.

Age. Late Devonian, late Famennian Stage (Fa2c substage); *Grandispora cornata* / *Rugispora flexuosa* palynomorph zone (Traverse, in press).

Etymology. Named for the truest friend of a supporter of our research.

Diagnosis. A small groenlandaspidid with a short head shield and tall and narrow dorsal trunk elements. The head shield is almost as wide as long (average W/L equals 0.96). The pineal is divided into two distinct plates in every specimen and the postmarginal makes contact with the postorbital plate, excluding the marginal plate from the lateral margin of the head shield. A continuation of the supraorbital sensory line reaches the caudal margin of the paranuchal plate. The PDL has an average H/L ratio of 2.42. The posterodorsal projection of the PDL is short and angled sharply upward so that the overlap zone for the MD does not reach the caudal margin of the element. The height of the symphysial area on the visceral surface of the PDL is 40% of the total height of the element. The MD is also high and narrow and approximately equal in height to the PDL.

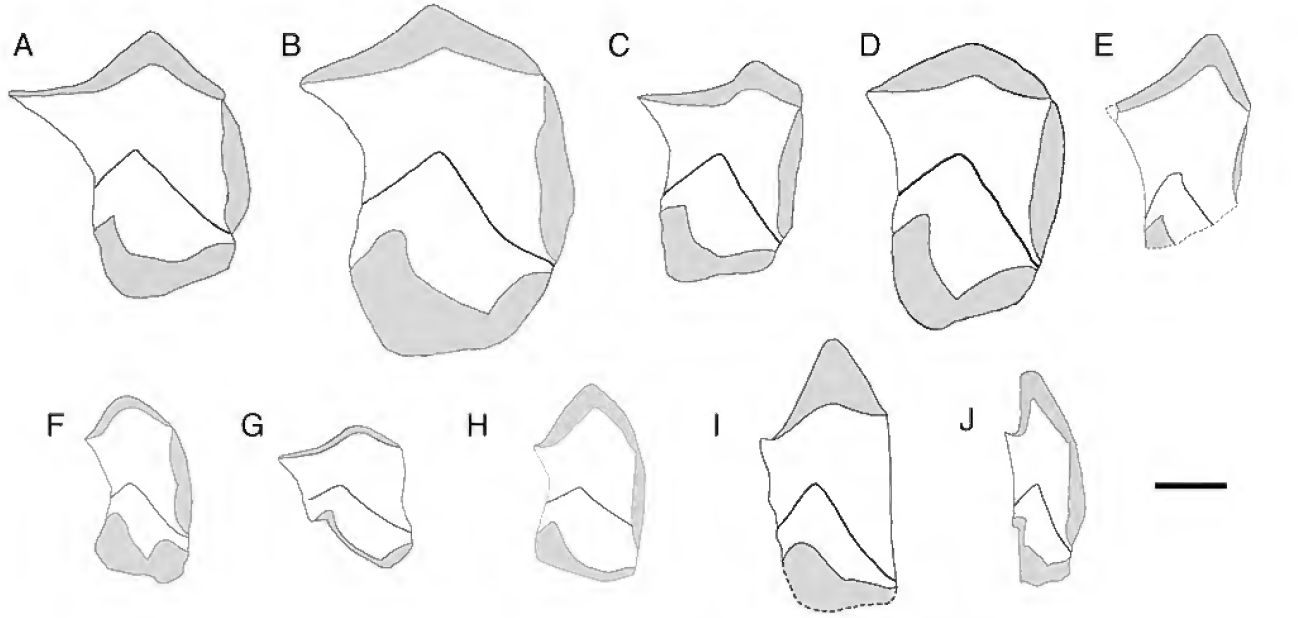


Fig. 5. Comparison of posterior dorsolateral plates (PDL) from groenlandaspidids. A, *Groenlandaspis pennsylvanica* n.sp.; B, *G. antarctica*; C, *G. disjectus*; D, *G. mirabilis*; E, *G. seni*; F, *G. riniensis*; G, *Boomeraspis goujeti*; H, *Tiaraspis subtilis*; I, *Africanaspis doryssa*; J, *Turrisaspis elektor* n.gen. and n.sp. Scale bar = 2 cm.

The MD has numerous coarse serrations along the caudal margin and tubercles on the lateral surfaces that form rows parallel to the ventral margin.

Description

Head Shield (Figs. 6–8, 11F). The pattern of sensory lines and bones in the head shield of *Turrisaspis elektor* is similar to other Late Devonian groenlandaspidids in which head shields are known (*Tiaraspis, G. riniensis*, and *G. antarctica*). The supraorbital sensory line begins in the centre of the rostral margin of each preorbital plate and terminates within the central plate. Unreported from other taxa, the supraorbital sensory line on some *Turrisaspis* specimens, including the holotype, re-appears just caudal to the middle of the central plate and continue across the paranuchal plate to the caudal margin of paranuchal where it terminates near the end of the main lateral line. The infraorbital sensory line starts where the orbit meets the postorbital plate and divides in the centre of the postorbital plate. The central sensory line, the medial branch of the infraorbital sensory line, extends onto the central plate and terminates there. The main lateral line, the lateral branch of the infraorbital sensory line, terminates at the caudal margin of the paranuchal plate.

ANSP 20705 (Fig. 7) preserves the head shield in 3-dimensions with parts of the lateral (AL) and ventral trunk shield (IL, AMV, AVL, and partial SP). The head shield of *Turrisaspis elektor* has a pineal plate that is divided into two separate elements, a character also seen in some undescribed Australian forms (A. Ritchie, pers. comm.). The APi is roughly square and has a distinct indentation in the centre of the visceral surface (see Fig. 8A,B). A similar indentation is seen on the Pi of *Groenlandaspis disjectus* (Ritchie, 1974) and *Tiaraspis subtilis* (Schultze, 1984). The PPi of *Turrisaspis elektor* is roughly triangular in ANSP 20705, but it is smaller and approaching oval-shaped in other specimens. The relative size and shape of the two pineal elements is variable among the sample of *Turrisaspis* head shields but two pineal elements are present in every specimen examined. Schultze (1984) illustrates a small single pineal in *Tiaraspis subtilis* and a space not covered by bone between the pineal and the rostral. It seems possible

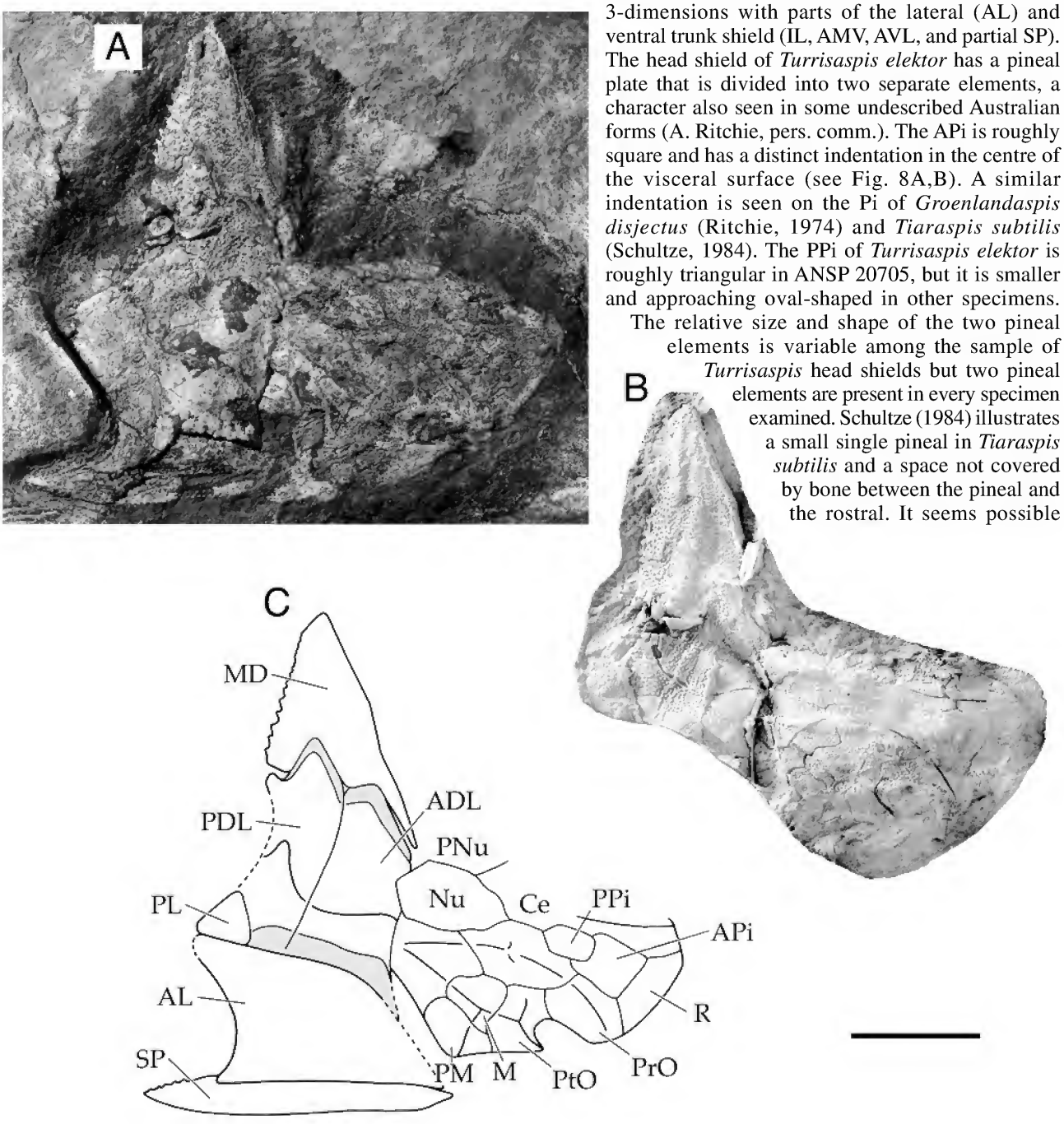


Fig. 6. *Turrisaspis elektor*, holotype, ANSP 20961, articulated specimen in right lateral view (head shield in dorsolateral view). *A*, specimen on matrix block; *B*, whitened latex peel made from counterpart block; *C*, line drawing of specimen using part and counterpart. Scale bar = 2 cm.

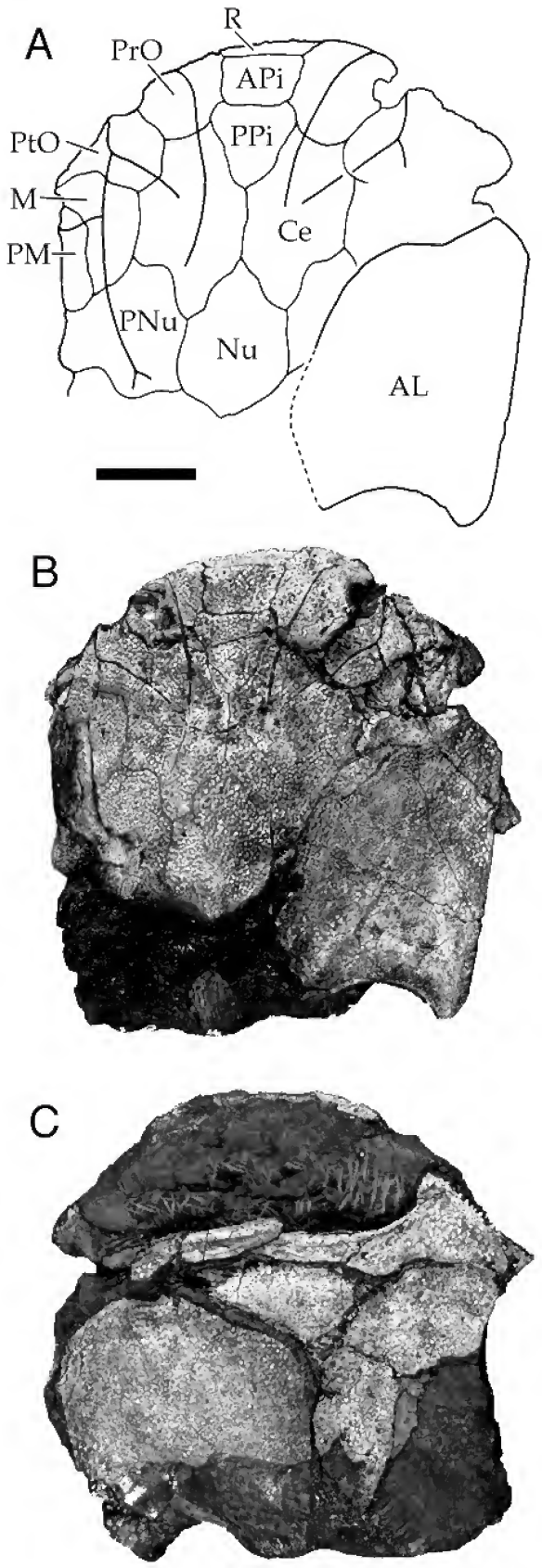


Fig. 7. *Turrisaspis elektor*, ANSP 20705. *A*, line drawing of head shield in dorsal view; *B*, dorsal view of head shield and anterior lateral plate; *C*, ventral view of head and partial trunk shield. Scale bar = 1 cm.

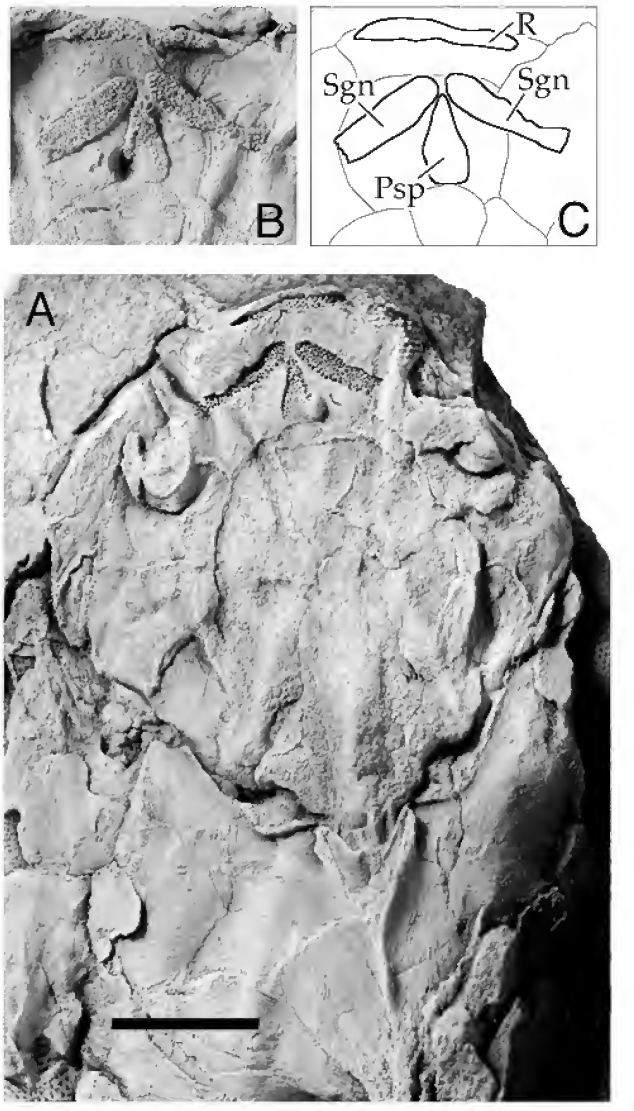


Fig. 8. ANSP 20748, *Turrisaspis elektor*. *A*, whitened, acid-prepared mold of the ventral surface of the dorsal head shield and medial surfaces of the lateral trunk shields; *B*, close-up of whitened latex peel of denticulated surfaces on the dermal bones of the palate; *C*, interpretive drawing of denticulated surfaces. Scale bar = 1 cm.

that two pineal elements may have been present in *Tiaraspis subtilis* but that the APi was missing from the specimen that Schultze (1984) described. This contention is perhaps contradicted by the presence of an indentation on the visceral surface of the APi of *Turrisaspis* and on the caudally placed Pi of *Tiaraspis*.

The pattern of head shield elements in *Turrisaspis* is quite like *Groenlandaspis antarctica* as illustrated by Ritchie (1975). *Turrisaspis* has a V-shaped caudal margin of the head shield unlike the relatively flat caudal margins of *Tiaraspis* and *G. riniensis*. The nuchal element in *Tiaraspis* narrows dramatically toward the caudal margin, unlike the others in this discussion. Unique to *Turrisaspis* among the known groenlandaspidid head shields is contact between the postmarginal and postorbital plates, excluding the marginal plate from the lateral margin of the head shield. In ANSP 20705 (Fig. 7) the marginal plate appears to reach the lateral margin on the left side of the head shield

but that is an artifact of crushing in that area. Ornamentation of evenly-spaced tubercles cover the entire head shield of *Turrisaspis elektor*.

Two specimens that were prepared by acid etching show details of the feeding apparatus on the dermal bones of the palate and rostrum. ANSP 20748 (Fig. 8A) includes a mold of the palatal surface showing four elongate, denticulated surfaces (Fig. 8A,B). The raised surface in the centre of the palatal area is interpreted as the ventral surface of the parasphenoid and the surfaces on either side of the parasphenoid are interpreted as supragnathals. The crescent-shaped, denticulated surface on the anterior-most margin of the mouth is interpreted as the anteroventral margin of the rostral plate (Fig. 8C). ANSP 21137 (not figured) shows the same morphology of feeding apparatus, although the denticulated surface on the ventral surface of the parasphenoid is broader.

Appendix 2 provides numerical data for the 10 measurable head shields of *Turrisaspis elektor* in the Red Hill sample. The specimens are usually flattened and thus distorted to varying degrees. The head shields in this sample show a range of lengths from 2.2 to 4.7 cm (measured from the anterior-most point on the rostral plate to the caudal-most point on the nuchal). The width of the head shields range from 2.2 to 4.3 cm (measured between the lateral-most points of the postmarginal plates). The head shield of *Turrisaspis* is almost as wide as long (average W/L equals 0.96). Other groenlandaspidid head shields (known from *Tiaraspis, G. riniensis*, and *G. antarctica*) have relatively longer skulls, but no statistical comparisons were done for this study.

Lateral Trunk Shield

ADL (Figs. 9G–I, 11C). The ADL of *Turrisaspis elektor* has a rhomboidal shape. The sample of seven measurable ADLs (listed in Appendix 2) shows variation in size and proportions of this element. The height of the ADL plates varies from 1.5 to 3.8 cm, and the average height/length ratio is 1.95 (measured as shown in Fig. 12). The dorsal and anteroventral margins are steep and the anteroventral and posterodorsal corners form acute angles. The anterodorsal margin of the ADL forms an angle of between 50° and 60° with the sensory canal. The caudal margin is concave where it overlaps the PDL. The ornamentation on the lateral surface consists of evenly distributed tubercles. There is a raised crest running from the condyle to the centre of the caudal margin (see Fig. 11C). This character is used by Long *et al.* (1997) to separate *Africanaspis* from *Tiaraspis*. A comparison of these high-spired taxa with *Turrisaspis* is presented below.

PDL (Figs. 9E,F; 11B). The PDL is tall and narrow, with an average height/length of 2.42. The sample of five measurable PDLs is listed in Appendix 2. The caudal margin of the PDL does not have the pronounced posterodorsal projection seen in the genus *Groenlandaspis* (Fig. 5). Instead, the caudal margin of the *Turrisaspis* PDL angles sharply upward at the posterodorsal corner of the element, creating a relatively vertical caudal margin and excluding the overlap zone of the MD from reaching the caudal margin. The posterior and anterior segments of the dorsolateral canal meet at an angle of 70°. Ornamentation of small tubercles are evenly distributed on the dermal surface of the element. In visceral view there is a tall, narrow symphysial area in the dorsal region of the PDL. The angle formed by this symphysial surface and the body of the PDL is about 30°, suggesting that the two sides of the trunk diverged at an angle of 60° from beneath the MD. The height of the symphysial surface is 40% of the height of the entire PDL.

AL (Figs. 9L–N, 11E). All specimens of the anterior lateral plate are longer than they are high. The sample of 11 measurable ALs is listed in Appendix 2. Height to length ratios vary from 0.55 to 0.83, with the higher ratios occurring in the smaller individuals such as ANSP 20947 (Fig. 9L). Shape change of the AL during ontogeny may indicate a change in the angle of the head shield relative to the trunk. The caudal margin is concave, and the cranial margin slopes steeply to a ventral point. The dermal surface has a raised crest that slopes upward from the anteroventral tip and changes angle cranial to the centre of the element, continuing to the posterodorsal corner of the element. The ornamentation on the dermal surface consists of tubercles that are evenly distributed or sometimes arranged in roughly concentric rows.

PL (Figs. 9J,K; 11D). The PL of *Turrisaspis elektor* is a small, triangular element with a large overlap zone ventrally for the dorsal lamina of the PVL and the AL. On the visceral surface there is a pronounced thickened rim along the ventral margin. The sample of seven measurable PLs is listed in Appendix 2. The ornament on the lateral surface consists of tubercles and crests.

MD (Figs. 9A–D, 11A). The MD of *Turrisaspis elektor* is high and narrow when compared to the genus *Groenlandaspis*. The apex of the MD makes an angle of 30° to 40°. Numerous coarse serrations line the caudal margin. The caudal margin of the MD is nearly vertical and sometimes actually slopes back so that the apex of the MD is the most posterior part of the element (Fig. 9D). In specimens with associated trunk shield elements, the height of the MD is roughly equal to the height of the PDL. The ornamentation on the MD consists of tubercles that are evenly distributed across most of the element or arranged in sinuous rows that are roughly parallel to the ventral margin.

The large sample size of MDs from *Turrisaspis elektor* (29 measurable specimens listed in Appendix 2) exhibits variation in size and shape. The large sample size provides an opportunity to confirm continuous variation within the sample and to examine intraspecific variation and ontogenetic change in this taxon. Figure 10 plots the height and length for the sample of measurable median dorsal plates of *Turrisaspis elektor* from Red Hill. Height was measured as the distance from the ventral margin of the MD (at the apex of the notch for the PDL) to the apex of the element. Length of the MD was measured perpendicular to the height measurement at the level of the apex of the notch for the PDL (see inset of Fig. 10). The distribution of points in Fig. 10 suggests that the size variation is continuous, arguing against an interpretation of more than one taxon within the sample, based on size. The variation around the best-fit line in Fig. 10 illustrates intraspecific and ontogenic variation in the shape of the MD, as captured by the simple

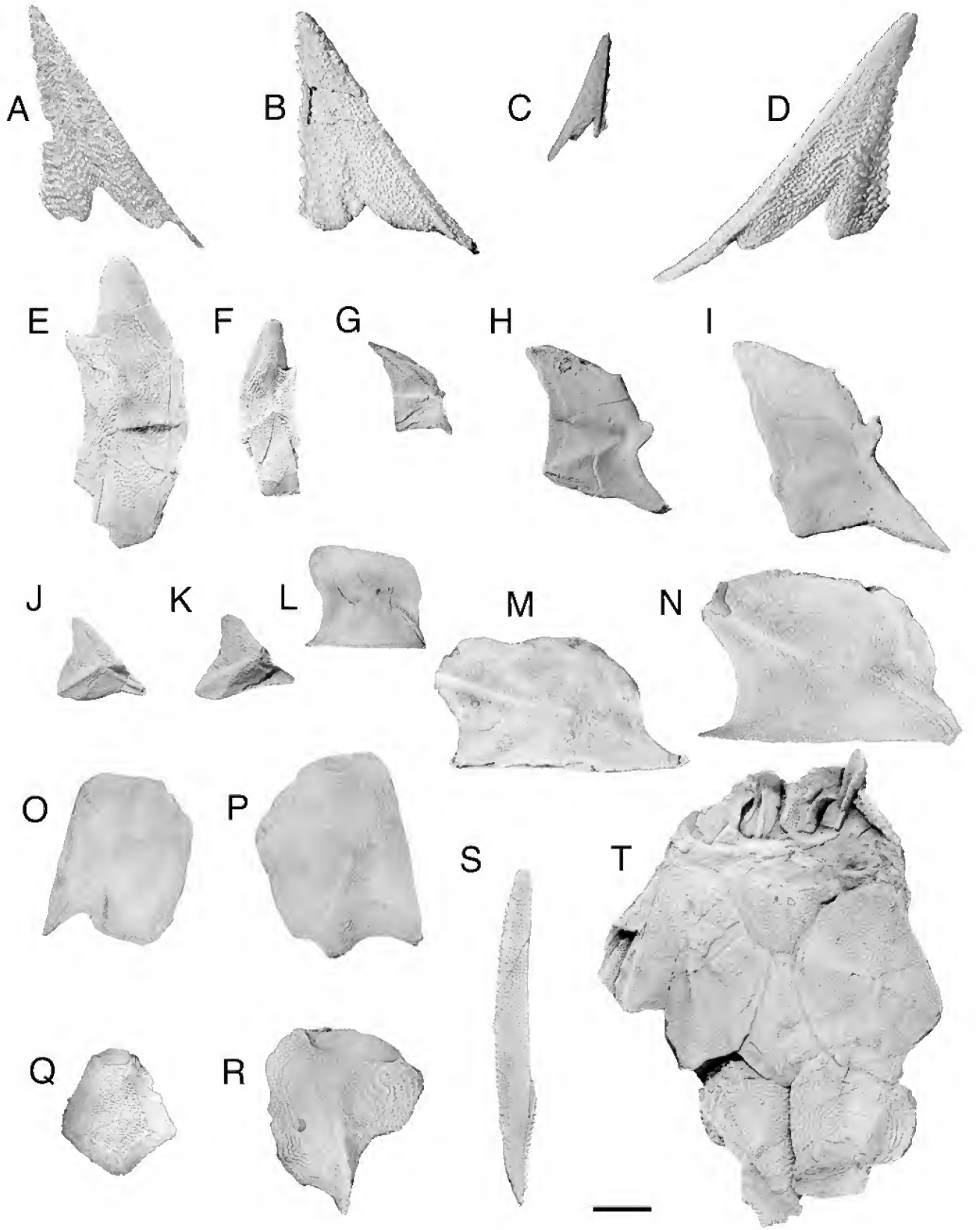


Fig. 9. Trunk plates of *Turrisaspis elektor*. Median dorsal plates (MD): *A*, ANSP 20687; *B*, ANSP 20714; *C*, ANSP 20707; *D*, ANSP 20703. Posterior dorsolateral plates (PDL): *E*, ANSP 20742, lateral aspect; *F*, ANSP 20741, lateral aspect. Anterior dorsolateral plates (ADL): *G*, ANSP 20946, lateral aspect; *H*, ANSP 20766, medial aspect; *I*, ANSP 20754, medial aspect. Posterior lateral plates (PL): *J*, ANSP 20952, lateral aspect; *K*, ANSP 20953, lateral aspect. Anterior lateral plates (AL): *L*, ANSP 20947, lateral aspect; *M*, ANSP 20726, lateral aspect; *N*, ANSP 21328, lateral aspect. Anterior ventrolateral plates (AVL): *O*, ANSP 20768, ventral aspect; *P*, ANSP 20681, ventral aspect. Posterior median ventral plate (PMV): *Q*, ANSP 20695, ventral aspect. Posterior ventrolateral plate (PVL): *R*, ANSP 20684, ventral aspect. Spinal plate (SP): *S*, ANSP 20770. Articulated ventral trunk shield: *T*, ANSP 20688A. All specimens whitened with ammonium chloride. Scale bar = 1 cm.

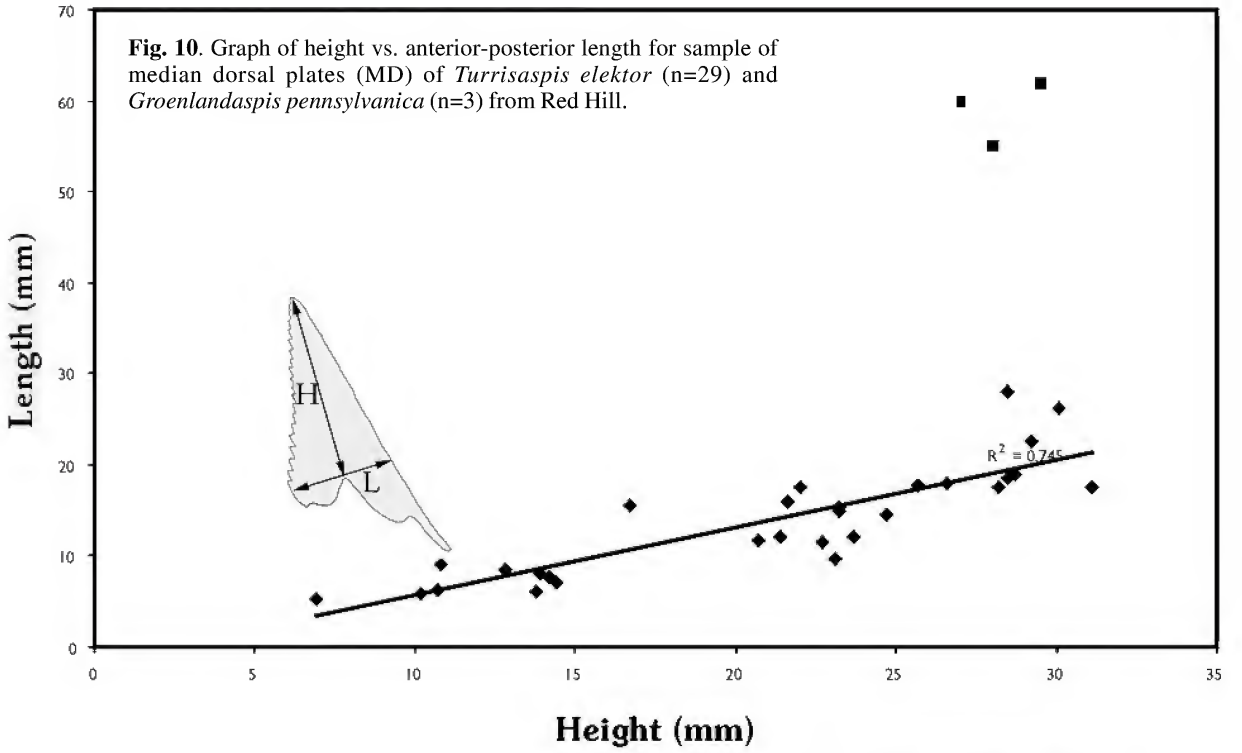
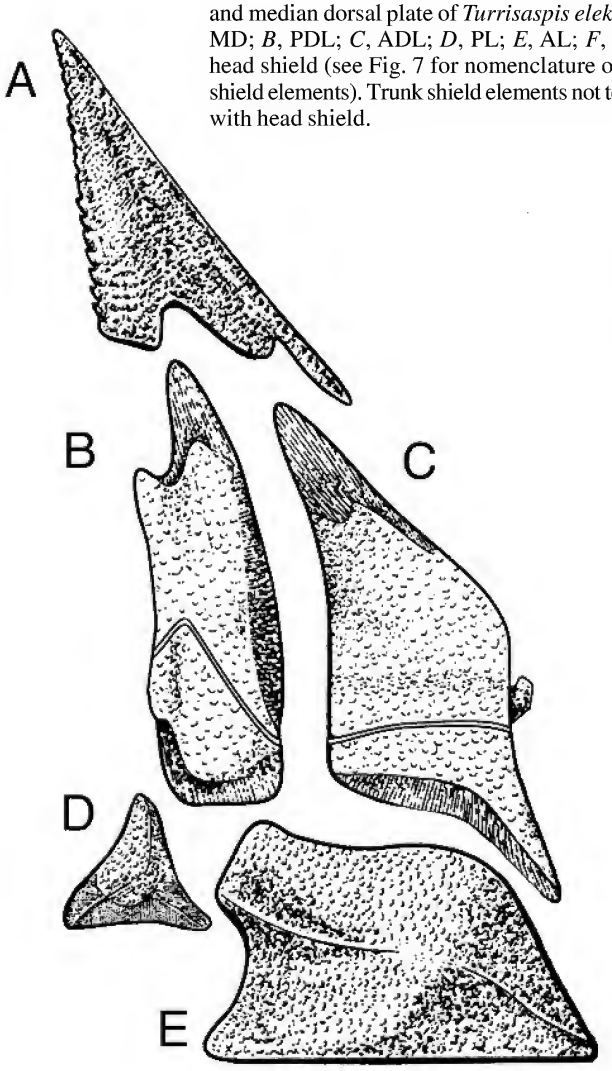


Fig. 10. Graph of height vs. anterior-posterior length for sample of median dorsal plates (MD) of *Turrisaspis elektor* (n=29) and *Groenlandaspis pennsylvanica* (n=3) from Red Hill.



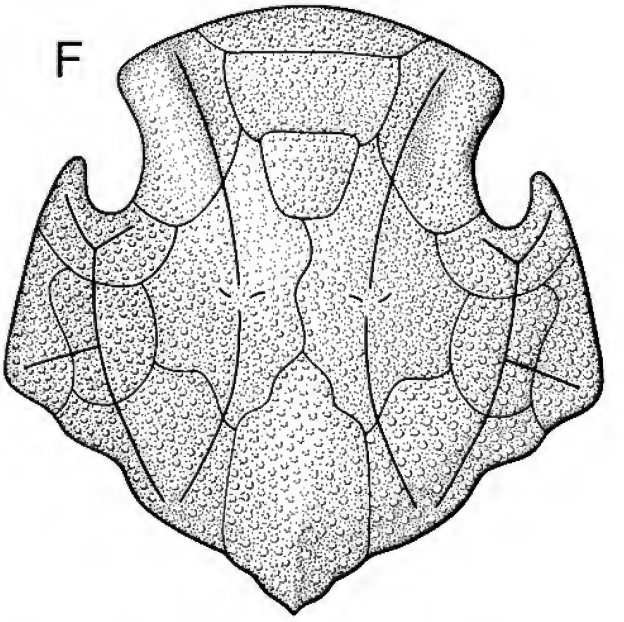


Fig. 11. Reconstructed headshield, lateral plates and median dorsal plate of *Turrisaspis elektor*: *A*, MD; *B*, PDL; *C*, ADL; *D*, PL; *E*, AL; *F*, dorsal head shield (see Fig. 7 for nomenclature of head shield elements). Trunk shield elements not to scale with head shield.

height and length measurements described above. Individual variation is also evident in the MD sample with respect to details of the serrations along the caudal margin, the development of ornament, and the slopes of the caudal and cranial margins (see Fig. 9A–D). Figure 10 also plots the three measurable specimens of the MD of *Groenlandaspis pennsylvanicus*. The distribution of these points clearly falls outside the range of variation in *Turrisaspis*.

Ventral Trunk Shield (Fig. 9T). The ventral trunk shield of *Turrisaspis elektor* is known from five articulated specimens and 23 measurable isolated elements. ANSP 20688A (Fig. 9T) is a well preserved example of an articulated ventral trunk shield. The pattern and relative proportions of the elements are like the ventral trunk shield of *Groenlandaspis antarctica* (Ritchie, 1975, fig. 2b),

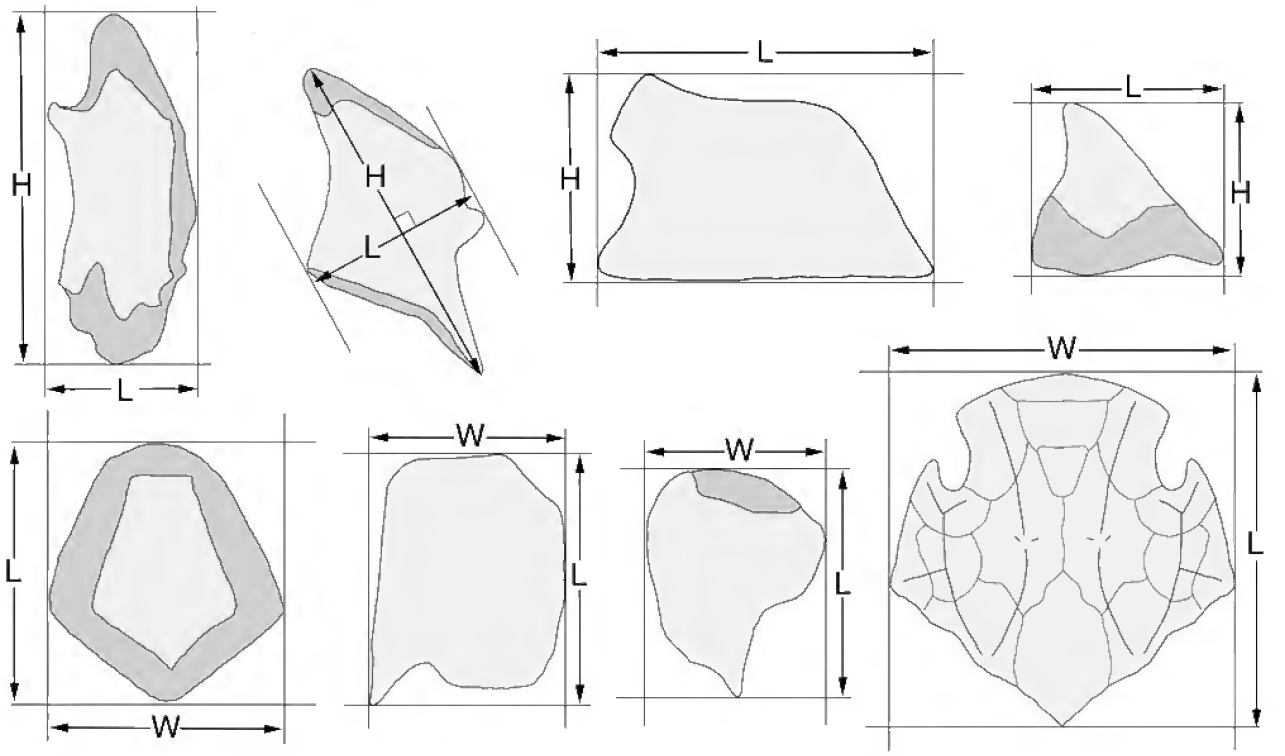


Fig. 12. Methods for deriving measurements of isolated trunk elements and head shields presented in Appendix 1 and 2.

although *Turrisaspis elektor* is significantly smaller.

AVL (Fig. 9 O,P). The AVL of *Turrisaspis elektor* is represented by 12 isolated specimens (list and measurements in Appendix 2). Within the sample of AVLs there is variation in the proportions of the element (width to length ratio varies from 0.62 to 1.0). The AVL has a straight lateral margin and a V-shaped depression that opens to the caudal margin. Ornamentation of fine tubercles are evenly distributed or arranged in rows following the margins of the plate.

PMV (Fig. 9Q). The PMV of *Turrisaspis elektor* is represented by seven isolated specimens (list and measurements in Appendix 2). The PMV is coffin-shaped, with a wide margin where it is overlapped from all sides. The PMV is ornamented with fine tubercles on the dermal surface.

PVL (Fig. 9R). The PVL of *Turrisaspis elektor* is represented by one isolated specimen (list and measurement in Appendix 2). On the cranial margin there is a distinct, crescent-shaped overlap area where the AVL overlaps the PVL. It appears that the left PVL overlaps the right PVL along part of the midline, although no isolated right PVL was present to observe the nature of the overlap area. The lateral flange of the PVL is angled at about 130° relative to the ventral portion of the plate. Ornamentation of fine tubercles are evenly distributed or arranged in rows following the margins of the plate.

SP (Fig. 9S). The SP of *Turrisaspis elektor* is represented by three isolated specimens. The spinal plate of *Turrisaspis elektor* is covered with tubercles that also cover the lateral margin, giving it a serrated appearance. Coarse, slightly forward-pointing serrations are particularly well developed along the medial margin at the caudal end of the SP. Data for the three measurable SPs are listed in Appendix 2. Width of the spinal plate was taken at the midpoint along its length.

Comparison to other groenlandaspidids

The large sample size for *Turrisaspis elektor* allows for recognition of variation in size and shape of the dermal elements. The authors feel justified in interpreting this material as a single taxon because the variation within each element is continuous as was demonstrated for the MD in Fig. 10. Although other elements have smaller sample size, they also exhibit continuous variation within different sized specimens. Importantly, this continuous variation in *Turrisaspis* does not extend to specimens that have been described as *Groenlandaspis pennsylvanica* and the adults of the two taxa are very different in size. Some elements such as the AL have similar shapes in the two taxa found at Red Hill and in these cases we may be unable to distinguish a juvenile of *G. pennsylvanica* from *T. elektor*. In other cases, elements such as the MD and PDL have very different shapes and ornament in each Red Hill taxon and identification of the two taxa is unambiguous.

The tall median dorsal plate of *Turrisaspis elektor* is similar to the tall MD plate seen in *Tiaraspis* sp. (Gross, 1965), *Tiaraspis subtilis* Gross, 1933, and *Africanaspis doryssa* Long *et al.*, 1997. The isolated, high-spired MDs of *Tiaraspis* sp. that were reported from the Late Devonian (Famennian) of Belgium by Gross (1965) have ornamentation of tubercles arranged in wavy rows and coarse serrations along the caudal margin, remarkably like the MD of *Turrisaspis*. Gross referred these Belgian specimens to *Tiaraspis* sp. but was skeptical about their provenance since the Famennian was beyond the known temporal range for *Tiaraspis*. The presence of the high-spired *Turrisaspis* from the Catskill Formation in Pennsylvania confirms that such forms were present in Euramerica during the Famennian

and may remove doubt about the provenance of the Belgian specimens. In *Turrisaspis* and *Tiaraspis subtilis* the MD is approximately the same height as the PDL. Many features of *Tiaraspis subtilis*, however, such as the shape of lateral trunk elements and the nature of the head shield elements are quite unlike *Turrisaspis elektor*. A close relationship between these two taxa is also improbable due to the long temporal gap between their occurrences. In *Africanaspis doryssa* the MD is about twice the height of the PDL and the symphysial surface on the visceral side of the PDL is nearly half of the height of the entire element (Long *et al.*, 1997). Although a raised crest running from the condyle of the ADL to the centre of the caudal margin is seen in both *Africanaspis* and *Turrisaspis*, the ADL and PDL of Africanaspis are not shortened cranially-caudally to the dramatic extent seen in *Turrisaspis*. Therefore, although *Turrisaspis elektor, Tiaraspis subtilis* and *Africanaspis doryssa* share the character of a tall MD with a H/L ratio greater than one, other aspects of their morphology suggest that they are not closely related. With the present knowledge of the phylogenetic relationships within groenlandaspidids it is not clear if a tall MD has evolved several times in groenlandaspidids or only once.

Turrisaspis elektor differs from all species of *Groenlandaspis* and from *Boomeraspis* by the high-spired MD, and the tall, narrow plates of the lateral trunk shield. Despite the fact that the dorsolateral plates of the trunk shield are quite unique in *Turrisaspis elektor*, the head shield and ventral trunk shield are similar to *Groenlandaspis antarctica*. This may indicate that *Turrisaspis* is more closely related to *Groenlandaspis* than to the high-spired, but otherwise distinctive, *Tiaraspis* and *Africanaspis*.

Discussion

The specimens described in this paper as two new species of groenlandaspidid placoderm were all recovered from within the 2-meter-thick fossiliferous zone at the Red Hill site. Within the fossiliferous zone, fossil material comes from two lithofacies that represent different sedimentary environments within a single fluvial system. The most fossiliferous lithofacies is the red, siltstone to fine sandstone beds that are gently-inclined as the result of deposition on shallow channel margins. Most fossil material from this lithofacies is disarticulated although not abraded, suggesting accumulation of slightly transported material near the channel margin. In one horizon within this lithofacies abundant articulated, although poorly preserved, *Turrisaspis* specimens suggest stranding in a temporary pool as water level fell. Specimens also occur in a laminated grey-green siltstone lithofacies that is interpreted as an overbank pond facies. Articulated specimens from each of these lithofacies suggest that groenlandaspidids lived in different environments, from shallow, quiet-water ponds to the active channels. The shear number of groenlandaspidid specimens recovered from the Red Hill site, relative to other taxa at Red Hill with similar preservation and collecting potentials, suggests that groenlandaspidid placoderms, particularly *Turrisaspis elektor*, were quite abundant in the fluvial environments represented at the site.

The sedimentology of the Red Hill site and, more generally, the sediments of the Duncannon Member of the Catskill Formation are indicative of deposition in freshwater fluvial environments within a subtropical, seasonal climatic regime (Woodrow, 1985; Woodrow *et al.*, 1995). Additionally, the presence of fragile terrestrial arthropods such as trigonotarbid arachnids (Shear, 2000) and large numbers of intact terrestrial plants reinforce the non-marine interpretation of the Red Hill site. The distinctly non-marine nature of the deposits at Red Hill is another example of the occurrence of groenlandaspidids in freshwater environments during the Famennian. Although most records of groenlandaspidids are from non-marine facies, several authors (e.g., Schultze & Cloutier, 1996; Anderson *et al.*, 1999) point out that groenlandaspidids are not exclusive to freshwater deposits and are therefore not reliable indicators of freshwater depositional conditions. In Pennsylvania, no trace of groenlandaspidids have been found in the downstream deltaic facies (Sherman Creek Member) of the Catskill Formation or in the contemporaneous Late Devonian marine facies of the Catskill Sea to the west.

Recognizing that *Groenlandaspis* and other groenlandaspidids may not be absolute indicators of non-marine depositional conditions, it nonetheless seems that they may cautiously be used for recognition of non-marine rocks in the Famennian. At Red Hill, and at Forbes, New South Wales, groenlandaspidids are found in the same faunas with early tetrapods. Thus, within the Famennian, groenlandaspidids may serve as useful environmental indicators for the kind of non-marine environments that favoured the preservation of early tetrapod fossils.

There are distinct similarities between *Groenlandaspis pennsylvanica* and other species of *Groenlandaspis* from Europe, Australia, and Antarctica. Such similarities argue for faunal exchange between the Euramerican and Gondwanan landmasses by the late Famennian. Palaeogeographic reconstruction such as Scotese & McKerrow (1990) that indicate a near-connection or connection between the two landmasses in the Late Devonian seems required to explain this biogeographic pattern. This pattern has been noted in Late Devonian freshwater vertebrates as well (e.g., Daeschler & Shubin, 1995, with early tetrapods; Ahlberg *et al.*, 2001, with the lungfish *Soederberghia*).

The genus *Groenlandaspis* has been recognized from Eifelian, Givetian, Frasnian and Famennian deposits within the Gondwanan landmasses and therefore does not have biostratigraphic utility in that province beyond marking these stages of the Middle and Late Devonian. Within the Euramerican landmass, however, the genus *Groenlandaspis* occurs only in Famennian strata (Lelievre & Goujet, 1986) and therefore marks that stage in remnants of the Euramerican Province. *Groenlandaspis pennsylvanica* and *Turrisaspis elektor* from Red Hill, Pennsylvania, can be confidently dated to the late Famennian Stage (Fa2c substage) based on palynomorphs. Thus, *Groenlandaspis pennsylvanica* is among the latest known species of *Groenlandaspis*. *Turrisaspis* may have a more restricted range but additional material from other sites, especially comparable material from the Famennian of Belgium mentioned by Gross (1965), needs to be described and a phylogenetic framework needs to be worked out to understand the diversity and interrelationships of groenlandaspidid taxa. Such an analysis is clearly needed so that biogeographic and biostratigraphic schemes can work with a clearer understanding of relationships within the family Groenlandaspididae.

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Appendix 1. *Groenlandaspis pennsylvanica*. Measurements (mm) of individual plates in the Academy of Natural Sciences, Philadelphia (ANSP). *H*, height; *L*, length.

ANSP	element	H	L	H/L
20753	MD	27.0	60.0	0.45
20755	MD	29.5	62.0	0.48
20777	MD	28.0	55.0	0.51
20727	AL	37.5	77.0	0.49
20940	AL	33.0	70.5	0.47
20740	AL	31.3	60.5	0.52
20743	ADL	66.0	36.2	1.8
20700	PDL	66.4	44.5	1.5
20955	PDL	60.0	44.0	1.4
21132	PDL	54.2	38.0	1.4
20725	PDL	62.5	53.0	1.2
21348	PDL	58.3	38.3	1.5

Appendix 2. *Turrisaspis elektor*. Measurements (mm) of individual plates in the Academy of Natural Sciences, Philadelphia (ANSP). *H*, height; *L*, length; *W*, width.

ANSP	element	H	L	H/L
20669	MD	23.1	9.7	2.4
20674	MD	12.8	8.4	1.5
20678	MD	13.8	6.1	2.3
20687	MD	31.1	17.6	1.8
20703	MD	28.2	17.6	1.6
20707	MD	14.2	7.6	1.9
20708	MD	10.7	6.3	1.7
20711	MD	24.7	14.5	1.7
20713	MD	30.1	26.2	1.1
20714	MD	28.5	18.5	1.5
20715	MD	29.2	22.5	1.3
20721	MD	10.2	5.9	1.7
20731	MD	10.8	9.0	1.2
20736	MD	21.4	12.2	1.8
20756	MD	21.6	16.0	1.4
20757	MD	20.7	11.7	1.8
20759	MD	26.6	17.9	1.5
20786	MD	14.4	7.1	2.0
20787	MD	28.5	28.1	1.0
20790	MD	23.2	14.9	1.6
20797	MD	23.2	15.4	1.5
20936	MD	13.9	8.1	1.7
20939	MD	22.0	17.6	1.3
20944	MD	6.9	5.3	1.3
20949	MD	22.7	11.5	2.0
20961	MD	16.7	15.5	1.1
21297	MD	28.7	19.0	1.5
21301	MD	25.7	17.7	1.5
21325	MD	23.7	12.2	1.9
20754	ADL	51.0	26.0	2.0
20764	ADL	32.0	16.0	2.0
20766	ADL	31.0	17.4	1.8
20789	ADL	14.9	8.4	1.8
20946	ADL	18.3	10.0	1.8
21322	ADL	38.5	22.5	1.7
21767	ADL	33.0	14.0	2.4
20741	PDL	27.0	10.3	2.6
20742	PDL	46.0	18.5	2.5
20761	PDL	32.5	14.2	2.3
20784	PDL	31.0	12.7	2.4
21136	PDL	41.3	17.7	2.3
20682	AL	19.5	24.9	0.78
20705	AL	21.6	31.3	0.69
20722	AL	15.9	24.2	0.66
20726	AL	19.3	35.0	0.55
20792	AL	18.7	30.8	0.61
20801	AL	16.8	27.5	0.61
20947	AL	15.0	18.0	0.83
20950	AL	20.8	26.5	0.78
20956	AL	15.9	24.2	0.66
21321	AL	16.7	27.7	0.60
21328	AL	21.7	34.2	0.63
20744	PL	22.0	22.0	1.0
20804	PL	14.0	16.0	0.88
20805	PL	13.4	14.9	0.90
20952	PL	12.8	14.0	0.91
20953	PL	13.0	15.6	0.83
20960	PL	20.0	23.0	0.87
21134	PL	9.0	11.6	0.78

ANSP	element	W	L	W/L
20672	AVL	28.0	38.6	0.73
20676	AVL	26.0	34.0	0.76
20680	AVL	12.6	12.6	1.0
20686	AVL	9.6	12.8	0.75
20698	AVL	18.8	22.9	0.82
20751	AVL	26.0	27.3	0.95
20752	AVL	29.0	29.9	0.99
20771	AVL	10.2	13.0	0.78
20791	AVL	22.7	34.7	0.65
21320	AVL	21.0	31.0	0.71
21418	AVL	17.6	28.6	0.62
21681	AVL	22.2	30.2	0.74
20683	PMV	10.3	13.0	0.79
20693	PMV	20.3	23.9	0.85
20695	PMV	19.0	20.0	0.95
20738	PMV	12.0	17.4	0.69
20937	PMV	17.3	21.0	0.82
20951	PMV	23.0	25.5	0.90
21331	PMV	18.4	22.0	0.84
20684	PVL	27.0	31.0	0.87
20720	SP	5.5	49.0	0.11
20770	SP	6.5	51.0	0.13
21144	SP	5.0	31.7	0.16
20673	head	24.4	29.6	0.82
20705	head	40.0	42.0	0.95
20747	head	27.0	30.0	0.90
20748	head	38.0	36.0	1.1
20799	head	43.0	41.1	1.0
20957	head	43.0	44.0	0.98
20961	head	43.0	47.0	0.91
21137	head	27.0	30.0	0.90
21188	head	24.6	22.0	1.1
21190	head	22.4	23.0	0.97

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The Genus *Elasmopus* (Crustacea: Amphipoda: Melitidae) from Mauritius (Indian Ocean) with Description of Five New Species

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ABSTRACT. Nine species of the genus *Elasmopus* collected in the intertidal and shallow-subtidal zone of Mauritius are described and figured. These comprise five species, *E. palu* n.sp., *E. pseudinteger* n.sp., *E. souillacensis* n.sp., *E. steelei* n.sp., *E. puteus* n.sp., which are new to science, two species, *E. menurte* J.L. Barnard and *E. spinimanus* Walker that are recorded from Mauritius for the first time and two species, *E. spinidactylus* Chevreux and *E. pectenicrus* (Bate) that were previously known from Mauritius. The genus *Elasmopus* is one of the most diverse genera of amphipods known from the island. A key to the *Elasmopus* species of Mauritius is provided.

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The genus *Elasmopus* is one of the most diverse melitid genera in the Indopacific tropics. Ledoyer (1978) recorded five species from Mauritius: *E. ecuadorensis hawaiensis* Schellenberg, 1938 (= ?*E. palu* n.sp.), *E. hooheno* J.L. Barnard, 1970 (= *E. pseudinteger* n.sp.), *E. molakai* [sic] *pilosus* Ledoyer, 1978, *E. pseudaffinis* Schellenberg, 1938 form A and B (clearly two species but neither apparently *E. pseudaffinis* Schellenberg) and *Elasmopus* sp. (insufficiently described and figured for any judgment to be made). Appadoo & Steele (1998) added a further three species, *E. pectenicrus* (Bate, 1862), *E. spinidactylus* Chevreux, 1908 and *Elasmopus* sp.

This paper reports on nine species of *Elasmopus* collected in Mauritius between 1998 and 2000, and includes five new species and two new records for the island. Taxonomic descriptions of the new species and figures and descriptions of previously unrecorded and recorded species are presented.

Material and methods

Amphipods were collected from algae, seagrass and coral rubble from 24 sites around the island of Mauritius from February 1998 to February 2000. All sites were visited at low tide and samples were collected from the intertidal and shallow subtidal zones. Algae and rubble were collected by scraping them from their substrates using a small hand trowel. Amphipods were collected using the formalin wash method (see Myers, 1985).

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Prior to dissection, the body length of amphipods was recorded by holding the body straight and measuring the length from the base of antenna 1 to the base of the telson. A stereomicroscope with a micrometre scale eyepiece was used for measuring.

Drawings were made using a Nikon compound microscope equipped with a drawing tube attachment.

Type material is deposited in the Australian Museum, Sydney (AM); specimens listed under accession numbers prefixed P are deposited in the AM. All other material is kept in the first author's (Chandani Appadoo) collection.

Abbreviations used in figures. A, antenna (1–2); C, coxa; D, dactylus (3–7); Ep, epimeron; G, gnathopod (1–2); L, labium; Md, mandible; Mx, maxilla (1–2); Mxp, maxilliped; P, pereopod (3–7); p, palp; T, telson; U, uropods (1–3).

Taxonomic section

Elasmopus menurte J.L. Barnard

Figs. 1, 2

Elasmopus menurte J.L. Barnard, 1974: 21, figs. 14, 15.
Elasmopus ecuadorensis hawaiensis.–Appadoo & Steele, 1998: 639.

Material examined. 1 juvenile from mixture of red coralline algae and the alga *Gracilaria salicornia*, Balaclava (20°3.7'S 57°30.7'E), 10 Sep. 1998. 1♀ from the alga *Enteromorpha flexuosa*, Flic-en-Flac (20°16.5'S 57°21.7'E), 9 Nov. 1998. 1♀, 1 juv., from *Gracilaria* sp., Souillac (20°31'S 57°30.7'E), 25 Mar. 1999. 3♂♂, 1♀, 2 juv., from mixture of the algae *Digenia simplex, Laurencia papillosa, Centroceras clavulatum, Padina* sp. and *Gracilaria salicornia*, Roches Noires (20°6.2'S 57°44.5'E), 9 Apr. 1999. 3♀♀ from mixture of *Padina* sp. and the alga *Halimeda* sp., Grand Baie (20°0.5'S 57°34'E), 5 May 1999. 1♀ from *Digenia simplex, Padina* sp. and the alga *Jania adherens*, Roches Noires, 21 Jun. 1999. 3♂♂, 4♀♀, 6 juv., from mixture of the algae *Laurencia papillosa, Padina* sp., *Digenia simplex, Dictyota divaricata* and *Jania adherens*, Trou D'eau Douce (20°14.5'S 57°47'E), 21 Jun. 1999. 1♂, 1 juv., from *Digenia simplex, Padina* sp. and *Jania adherens*, Roches Noires, 6 Aug. 1999. 2♂♂, 3♀♀ from *Ulva lactuca*, Palmar (20°13.5'S 57°48'E), 6 Aug. 1999. 1♂, 1♀ from the alga *Sargassum* sp., La Cuvette (20°00'S 57°34.2'E), 12 Oct. 1999. 7♂♂, 28♀♀, 12 juv. from mixture of *Digenia simplex, Padina* sp. and globose brown algae, Roches Noires, 15 Oct. 1999. 1♀ from mixture of *Padina* sp., *Sargassum densifolium*, the alga *Pocockiella variegata* and globose brown alga, Bain Boeuf (19°59'S 57°36'E), 13 Dec. 1999. 1♂, 4♀♀, from mixture of *Padina* sp., *Digenia simplex, Sargassum* sp., globose brown alga, Roches Noires, 16 Dec. 1999.

Description. Male: length 6.7 mm. Head, lateral cephalic lobes rounded, with subocular notch, eyes large and subround with ring of clear ommatidia surrounding a dark core. Antenna 1, peduncle article 1 with robust seta and a few slender setae on posterior margin; article 2 subequal to 1; article 3, 0.6× length of article 1; accessory flagellum 3-articulate, the third article vestigial; primary flagellum 21-articulate. Antenna 2, peduncle articles 4 and 5 setose; article 5, 0.8× length of article 4; flagellum 7-articulate. Mandible, palp article 2, 1.5× article 1, with several medial and several distal setae; article 3 falcate, subequal to article 2, with comb row of setae, 2 long apical setae and 2 shorter setae on anterior margin. Maxilla 1, inner plate with 2 terminal plumose setae and several fine setae on inner margin. Labium, with rounded mandibular lobes; outer plate with blunt stout seta on inner margin. Maxilliped, palp article 3 with a small distal protuberance. Gnathopod 1, coxa produced anterodistally, rounded, 1.6× as long as broad, distal margin with very short setae; basis twice as long as broad; propodus slightly longer than carpus, with 2 distinct semicircular comb rows of setae on inner medial face, palm defined by a robust seta. Gnathopod 2, coxa about 1.5× as long as broad, distal margin with short setae; basis 3× as long as broad; merus posterodistal margin weakly produced, carpus twice as broad as long; propodus about 5× as long as carpus, posterior margin densely setose, distal part of palm with robust setae on a shallow protuberance; inner medial face of propodus with a small ridge carrying robust setae; dactylus about half length of propodus, inner margin weakly crenulate. Pereopods 3–4, coxa distal margin with short setae; propodus 1.2× as long as carpus, posterodistal margin with 1 long and 1 short straight robust seta; dactylus subdistally constricted. Pereopods 5–7, basis weakly serrate with short setae. Pereopods 5–6, basis posterior margin weakly convex, posterodistal margin produced into a rounded lobe. Pereopod 7, basis posterior margin strongly convex, posterodistal corner subtriangular. Epimera 1–3, with weakly developed posterodistal tooth, distal margin with a single row of 1 to 3 robust setae. Epimeron 3 subquadrate. Pleon and urosomite 1, with short fine dorsal setae. Urosomite 1, with a low, triangular, dorsal hump. Uropod 1, peduncle 1.2× length of inner ramus; outer ramus subequal in length to inner ramus. Uropod 2, peduncle subequal to inner ramus; outer ramus 1.2× length of inner ramus. Uropod 3, peduncle subequal to inner ramus; outer ramus 1.2× length of inner ramus; both rami with robust setae on lateral margin; outer ramus truncate, with terminal robust setae and 1 long slender seta. Telson, cleft to about 75% its length; telsonic lobes notched and with two to three robust distal setae.

Female sexually dimorphic characters: length, 4.7 mm (with oostegites). Gnathopod 1, similar to that of male but basis more slender, 3× as long as broad; propodus subequal to carpus. Gnathopod 2, coxa subquadrate 1.6× as long as broad, posterior margin with short robust setae; basis 3× as long as broad; propodus 1.8× as long as carpus, twice as long as broad, posterior margin with long slender setae, palmar border with stout robust setae interspersed between long slender setae.

Variation. The telson apices are asymmetrical (inner tooth more produced than the outer) in large males (e.g., 6.7 mm) but symmetrical in juveniles (e.g., 4.3 mm).

Remarks. This is the first record of *E. menurte* from Mauritius. Present material agrees closely with the description of J.L. Barnard (1974). The species is distinguished from all other *Elasmopus* species in Mauritius by the following characters in combination: the short setae on the coxal plates of gnathopods 1 and 2, the presence of robust setae on a protuberance on the palm of the male gnathopod 2, the simple robust setae on the posterodistal margin of the propodus of pereopods 3 and 4, the shape of the telson and the presence of a small hump on urosomite 1.

Type locality. Western Australia, west of Bunker Bay, Cape Naturaliste.

Distribution. Western Australia; Mauritius.

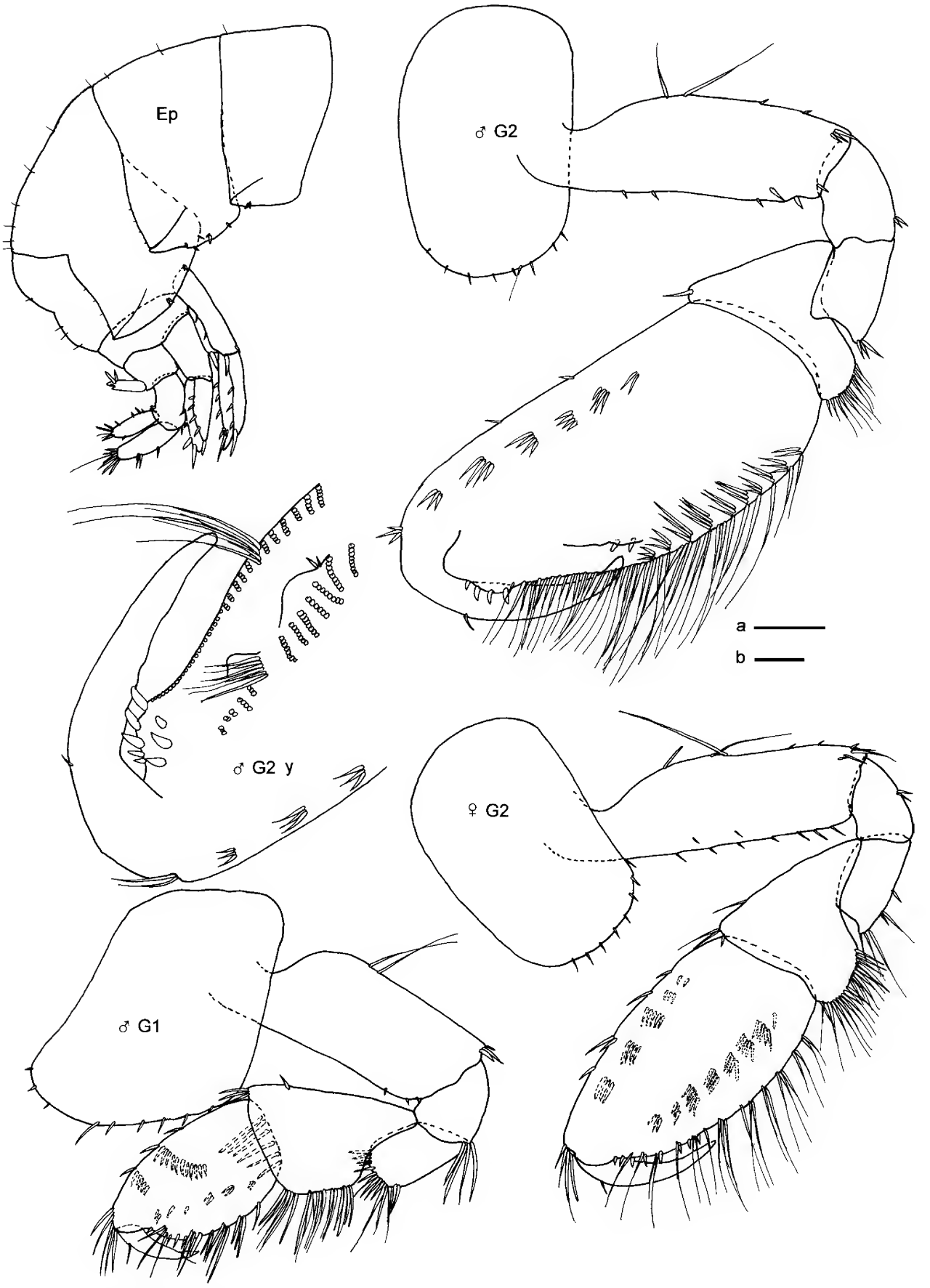

Fig. 1. *Elasmopus menurte* J.L. Barnard: ♂, 6.2 mm, Palmar, scale *a* = 0.4 mm (*Ep*); ♂, 6.7 mm, Trou D'eau Douce, scale *b* = 0.1 mm (*G2y*); ♂, 4.3 mm, Roches Noires, scale *b* = 0.1 mm (*G1–2*); ♀, 4.7 mm, Roches Noires, scale *b* = 0.1 mm (*G2*).

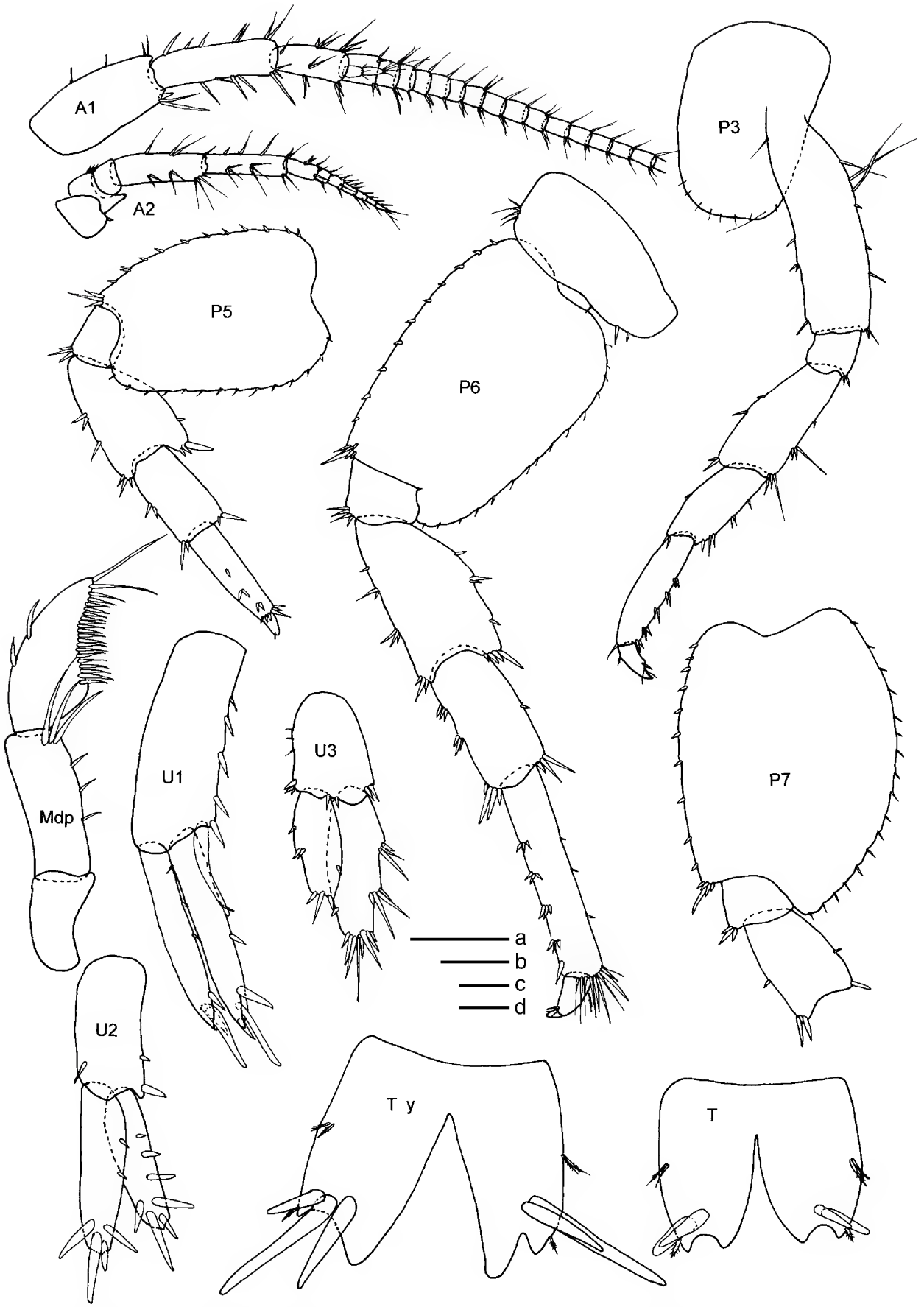

Fig. 2. *Elasmopus menurte* J.L. Barnard: ♂, 4.3 mm, Roches Noires, scales *a* = 0.4 mm (*A1–2*), *b* = 0.2 mm (*P3, P5–7*), *c* = 0.1 mm (*U1–3*), *d* = 0.05 mm (*Mdp, T*); ♂, 6.7 mm, Trou D'eau Douce, scale *d* = 0.05 mm (*Ty*).

Elasmopus palu n.sp.

Fig. 3

?*Elasmopus ecuadorensis hawaiensis*.–Ledoyer, 1978: 269, fig. 27.

Type material. HOLOTYPE: ♂, 2.5 mm (slides and carcass) from *Padina, Pocockiella variegata* and coral rubble, Flic-en-Flac (20°16.5'S 57°21.7'E), 10 Dec. 1999, AM P60543. PARATYPES: 2♀♀, same data as holotype, AM P60542.

Description. Male: Length, 2.5 mm. Head, with subocular notch; eyes large, oval with well-developed ring of clear ommatidia surrounding a dark central core. Antenna 1, peduncle article 2 subequal to 1; article 3, 0.5× article 1; accessory flagellum 1-articulate; primary flagellum 14-articulate, the terminal article rudimentary. Antenna 2, article 5, 0.9× article 4; flagellum 7-articulate. Mandible, palp article 2 with 1 small medial and 2 distal setae; article 3 falcate, 1.2× article 2 with comb row of setae and 4 long apical setae. Maxilla 1, inner plate with 2 terminal plumose setae, and several fine setae on inner margin. Labium, with mandibular lobes acute; outer plate with a blunt stout seta on inner margin. Maxilliped, palp article 3 with a small distal protuberance. Gnathopod 1, coxa 1.5× as long as broad, weakly produced anterodistally, distal margin with short setae; basis 2.3× as long as broad; propodus 1.2× carpus, palm defined by a stout robust seta. Gnathopod 2, coxa 1.8× as long as broad, distal margin with short setae; basis 2.8× as long as broad; carpus cup-shaped, twice as broad as long; propodus 3.7× carpus, 1.9× as long as broad, posterior margin densely setose, setae longest proximally but reducing in length sequentially towards distal end, palm a short shelf followed by a concavity, inner face of propodus with a small ridge bearing short robust and fine setae; dactylus about half length of propodus. Pereopod 3–4, coxa with short setae on distal margin; propodus posterodistal margin with 1 curved striate sabre seta and 1 straight robust seta. Pereopod 5–7, basis posterior margin castellate with short setae. Epimera 1–3, with a row of robust setae on the anterodistal margin. Epimeron 3, posterodistal margin with 2 teeth. Uropod 1, peduncle subequal to inner ramus; outer ramus 0.9× inner ramus. Uropod 2, outer ramus 0.8× inner ramus. Uropod 3, peduncle 1.3× inner ramus; inner ramus twice as long as broad, 0.6× outer ramus. Telson, cleft to about 75% its length, with notched and broadly sinuous apices, each with 2 robust setae.

Female secondary sexual characters: length, 2.9 mm (ovigerous). Gnathopod 1, similar to that of male but basis 2.5× as long as broad. Gnathopod 2, coxa 1.7× as long as broad; basis 3× as long as broad; carpus 1.4× as long as broad; propodus twice as long as carpus, 2.2× as long as broad, palm oblique, defined by a robust seta.

Remarks. *Elasmopus palu* n.sp. resembles *E. lapu* Myers (1985), but differs in several ways: in *E. palu*, the distal margins of coxa 1 and 2 lack dense long setae, the flagellum of antenna 1 is 14-articulate (20-articulate in *E. lapu*), the carpus of the male gnathopod 2 is less compressed and epimeron 3 has two teeth on the posterodistal margin, which are lacking in *E. lapu*. *Elasmopus lapu* reaches 5.5 mm whereas *E. palu* is only 2.5 mm in the male and 2.9 mm in the female. The species described by Ledoyer (1978) from Mauritius under the name *Elasmopus ecuadorensis hawaiensis* closely resembles *E. palu*. Similarities include the development of a tooth on the inner face of the posterior margin of the male gnathopod 2 propodus (better developed in Ledoyer's figures) and a strong almost transverse palmar shelf, the presence of two small teeth on the posterodistal corner of epimeron 3, the unequal uropod 3 rami and the shape of the basis of pereopods 5–7. The only difference is the presence of long setae on coxae 1–2 of Ledoyer's specimens and the precise allocation of this material must await further study.

Type locality. Flic-en-Flac, Mauritius.

Distribution. Mauritius.

Etymology. An anagram of "lapu" recording its close similarity to *Elasmopus lapu* Myers, 1985.

Elasmopus pectenicrus (Bate)

Fig. 4

Maera pectenicrus Bate, 1862: 192, pl. 34(8).
Elasmopus pectenicrus.–K.H. Barnard, 1916: 197, pl. 28(33).–K.H. Barnard, 1940: 461.–Schellenberg, 1928: 647; 1938: 55.–Shoemaker, 1935: 238.–Pirlot, 1936: 312.–Ruffo, 1938: 162; 1969: 28.–Reid, 1951: 236, fig. 32.–J.L. Barnard, 1955: 8, fig. 4.–J.L. Barnard, 1970: 126, figs. 73, 74.–Nayar, 1959: 27, pl. 9(20–35).–Sivaprakasam, 1966: 103.–Griffiths, 1974a: 235; 1974b: 289; 1975: 121.–Ledoyer, 1982: 475, figs. 179, 180a.–Appadoo & Steele, 1998: 639.

Material examined. 1♂ from the alga *Centroceras clavulatum*, la Cuvette (20°00'S 57°34.2'E), 28 Aug. 1999. 3♂♂ from mixture of the algae *Sargassum* sp., *Ulva reticulata, Digenia simplex* and *Centroceras clavulatum*, La Cuvette, 25 Jan. 2000.

Description. Male: length, 6.2 mm. Head, with subocular notch; eyes oval, with ring of clear ommatidia and a dark central core. Antenna 1, peduncle article 1 with few setae; article 2 subequal to 1; article 3, 0.7× article 1; accessory flagellum 2-articulate; primary flagellum 20-articulate. Antenna 2, peduncle articles 4 and 5 setose; article 5 slightly longer than article 4, flagellum 10-articulate. Mandible, palp article 2 twice as long as article 1, with setae on medial and lateral surfaces; article 3 falcate, 1.2× article 2, with comb-row of setae and 4 long apical setae. Maxilla 1, inner plate with 2 terminal plumose setae and several fine setae on inner margin. Labium, mandibular lobes rounded; outer plate with a small blunt stout seta on inner margin. Maxilliped, palp article 3 with a small protuberance at distal end. Gnathopod 1, coxa expanded anterodistally, 1.2× as long as broad, distal margin with very short setae; basis almost 3× as long as broad, posterior margin with patches of long setae; carpus 1.2× length of propodus with dense medial rows of long pectinate setae; propodus 1.5× as long as broad, anterior margin with 6 groups of setae, palm defined by a short robust seta. Gnathopod 2, coxa 1.2× as long as broad, distal margin with short setae; basis 3.4× as long as broad; carpus reduced, about 2.2× as broad as long; propodus 6× as long as carpus, palm short, almost transverse, posterior margin sinuous, with dense pectinate setae along almost entire length; dactylus slender, evenly curved. reaching about half length of propodus. Pereopods 3–4, basis slender, 4× as long as broad; propodus posterodistal margin with 1 long and 1 short straight robust seta; dactylus

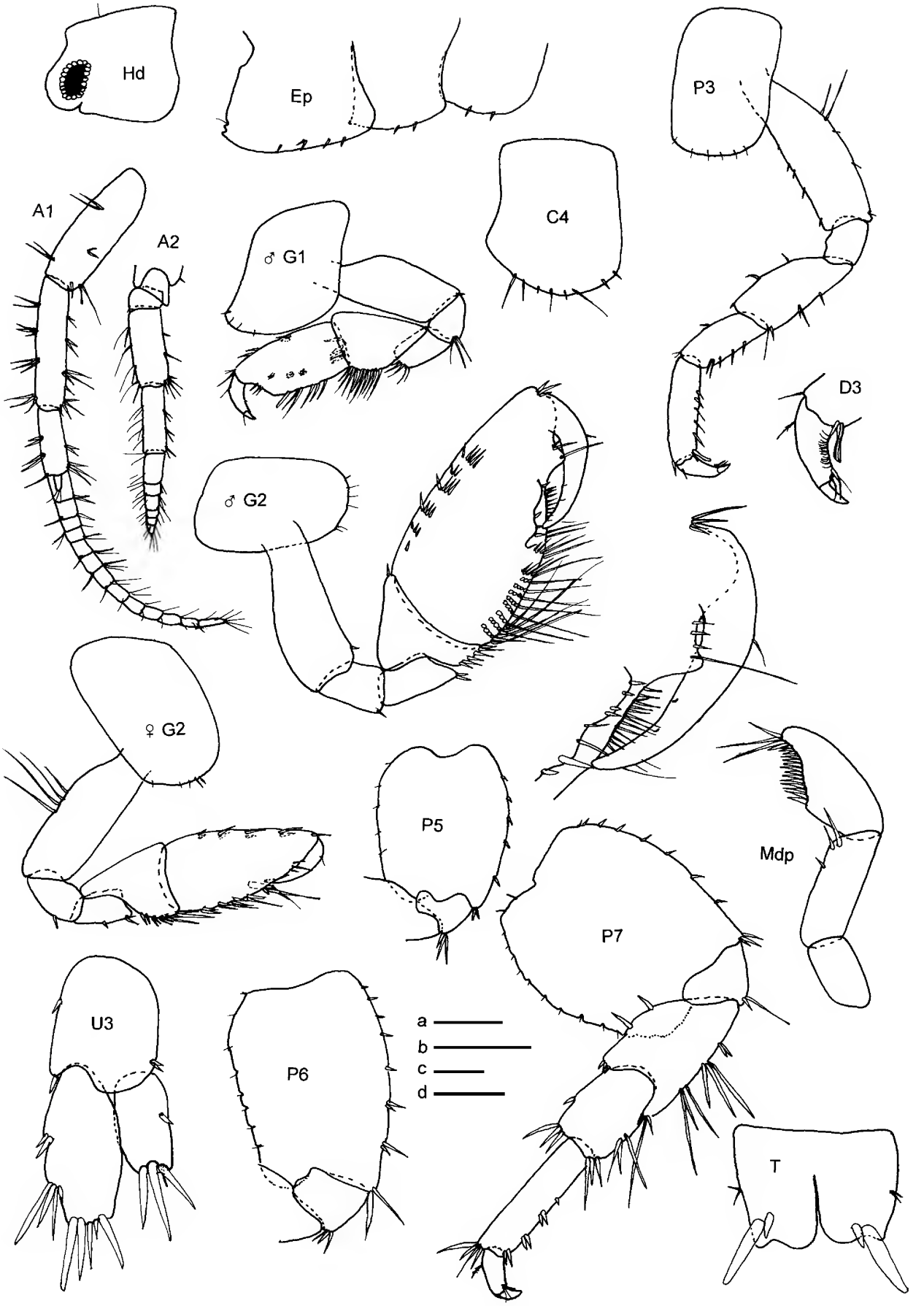

Fig. 3. *Elasmopus palu* n.sp.: ♂, 2.5 mm, Flic-en-Flac, scales *a* = 0.2 mm (*Hd, A1–2, Ep*), *b* = 0.2 mm (*G1, G2, P3, C4, P5–7*), *c* = 0.05 mm (enlargement of *G2, D3, U3*), *d* = 0.05 mm (*Mdp*); ♀, 2.9 mm, Flic-en-Flac, scales *b* = 0.2 mm (*G2*), *d* = 0.05 mm (*T*).

constricted subdistally. Pereopod 5, basis subovate, posterior margin weakly crenulate with short setae. Pereopod 6, basis posterior margin convex, produced into a subtriangular distal lobe, posterodistal margin deeply castelloserrate. Pereopod 7, basis posterior margin strongly convex, weakly castelloserrate with short setae. Epimera 1–2, with small posterodistal tooth. Epimeron 3, posterodistal margin weakly serrate, distal margin with row of robust setae in groups of 1–3. Uropod 1, outer ramus 0.7× length of peduncle and slightly shorter than inner ramus. Uropod 2, peduncle subequal to outer ramus; outer ramus 0.8× inner ramus. Uropod 3, peduncle subequal to inner ramus; inner ramus 0.7× length of outer ramus; rami truncate with robust setae on lateral margins and on apices. Telson, cleft 75% its length, apically truncate with 4 robust setae on each lobe.

Female. Not found.

Remarks. This species can be distinguished from the other *Elasmopus* species in Mauritius by the following characters in combination: short setae on coxae of gnathopods 1 and 2, the shape of gnathopod 2 with a long slender dactylus, the castelloserrate and triangular process on the basis of pereopod 6 and the truncate and spinous telson.

Type locality. New Guinea (see Bate, 1862).

Distribution. West Africa, South Africa, Madagascar, Mauritius, Red Sea, India, Indonesia, New Guinea, Australia, Hawaii, Caribbean.

Elasmopus pseudinteger n.sp.

Figs. 5, 6

Elasmopus hooheno.–Ledoyer, 1978: 269.–Appadoo & Steele, 1998: 639.

Not *E. hooheno* J.L. Barnard, 1970: 121, fig. 70.

Type material. HOLOTYPE: ♂, 5.2 mm, from the alga *Acanthophora spicifera*, Anse la Raie (19°59.5'S 57°37.5'E), 15 May 1998, AM P60544. PARATYPES: 5♂♂, 8♀♀, same data as holotype, AM P60545.

Additional material examined. 1♂, 3♀♀, 5 juv., from *Acanthophora spicifera*, Anse la Raie, 15 May 1998. 6♂♂, 6♀♀, 5 juv., from *Jania* sp. and *Valonia* sp., Bain Boeuf (19°59'S 57°36'E), 28 Aug. 1998. 6♀♀, 5 juv., from mixture of *Caulerpa racemosa, Digenia simplex* and *Jania adherens*, Roches Noires (20°6.2'S 57°44.5'E), 9 Apr. 1999. 1♂, 3♀♀, 4 juv., from *Laurencia papillosa*, Anse la Raie, 24 Jan. 2000. 1♂, 5♀♀, 1 juv., from mixture of *Padina* sp., *Gracilaria salicornia, Ulva lactuca, Hypnea cornuta* and *Dictyota divaricata*, Choisy (20°01'S 57°32.7'E), 25 Jan. 2000.

Description. Male: Length, 3.9 mm. Body, with 1 or 2 groups of setae on dorsum, pereon and pleon. Head, with rudimentary subocular notch; eyes large and subround with ring of clear ommatidia and a dark core. Antenna 1, peduncle articles 1 and 2 subequal; article 3, 0.6× article 1; accessory flagellum 1-articulate; primary flagellum 19-articulate. Antenna 2, articles 4 and 5 subequal; flagellum 7-articulate. Mandible, palp article 2 with 1 medial and 2 distal setae; article 3 falcate, 1.4× article 2, with comb row of setae and 3 long terminal setae. Maxilla 1, inner plate with 2 terminal plumose setae and fine setae on inner margin. Labium with mandibular lobes acute; outer plate with blunt stout seta on inner margin. Maxilliped, palp article 3 with a small protuberance at distal end. Gnathopod 1, coxa subquadrate, 1.2× as long as broad, distal margin with setae reaching abut half length of coxa; basis slightly expanded, 2.3× as long as broad, with a group of long setae on the posterior margin; propodus subequal to carpus, palm defined by a robust seta, anterior margin with 2 groups of setae. Gnathopod 2, coxa 1.3× as long as broad, distal margin with a group of setae about half the length of the coxa; basis 2.2× as long as broad, posterior margin with 4 long setae, distal end of anterior margin with about 5 robust setae; carpus cup-shaped, twice as broad as long; propodus 4× length of carpus, narrower distally, posterior margin poorly setiferous, inner face with 2 distal processes and 1 medial process between which is a pit for reception of the dactylar tip; dactylus falciform. Pereopods 3–4, basis 3.2× as long as broad; propodus posterodistal margin with 1 striate sabre seta and 1 normal robust seta; dactylus distally constricted. Pereopod 5, basis broad, posterior margin crenulate distally, with both short and very long setae; merus and carpus expanded, about as broad as long. Pereopod 6, basis almost as broad as long, posterior margin crenulate distally, with short and very long setae. Pereopod 7, basis posterior margin convex, crenulate with short and very long setae. Epimeron 1, subquadrate. Epimeron 2, posterodistal margin produced into a small tooth, distal margin with a few setae. Epimeron 3, posterodistal margin weakly scalloped with short setae, distal margin with several well-developed setae. Uropod 1, peduncle 1.3× rami; rami subequal. Uropod 2, peduncle subequal to inner ramus; inner ramus 1.1× outer ramus. Uropod 3, peduncle subequal to outer ramus; outer ramus 1.2× inner ramus; inner ramus with only terminal robust setae. Telson, subquadrate, as long as broad, uncleft, with 2 stout robust setae on each side.

Female secondary sexual characters: length, 3 mm (ovigerous). Gnathopod 1, coxa a little deeper and basis a little longer than that of male; propodus 1.2× length of carpus. Gnathopod 2, coxa 1.5× as long as broad; basis 2.7× as long as broad; propodus 1.8× carpus; palmar margin with defining robust seta.

Remarks. This species closely resembles *Elasmopus integer* Myers (1989) from the Society Islands. However, *Elasmopus pseudinteger* differs from *E. integer* in the 1-articulate accessory flagellum (two articulate in *E. intiger*); the more slender mandibular palp with less setiferous article 2; the more setiferous basis of pereopods 5 to 7; the scalloped posterodistal margin of epimeron 3 (evenly convex with small posterodistal tooth in *E. integer*)and in the evenly convex posterior margin of the telson (with dorsodistal depression in *E. integer*).

An entire (uncleft) telson is known only in two other species of *Elasmopus, E. integer* Myers from the Society Islands and *E. takamotus* Myers (1986) from Niue Island. *Elasmopus pseudinteger* is thus easily distinguished from all other *Elasmopus* species in Mauritius.

Habitat. This species was found mostly among red algae along the north and northeast coast of Mauritius.

Type locality. Anse la Raie, Mauritius.

Distribution. Known only from Mauritius.

Etymology. From the Latin *pseudo*—false and *integer*, the name of a closely related species.

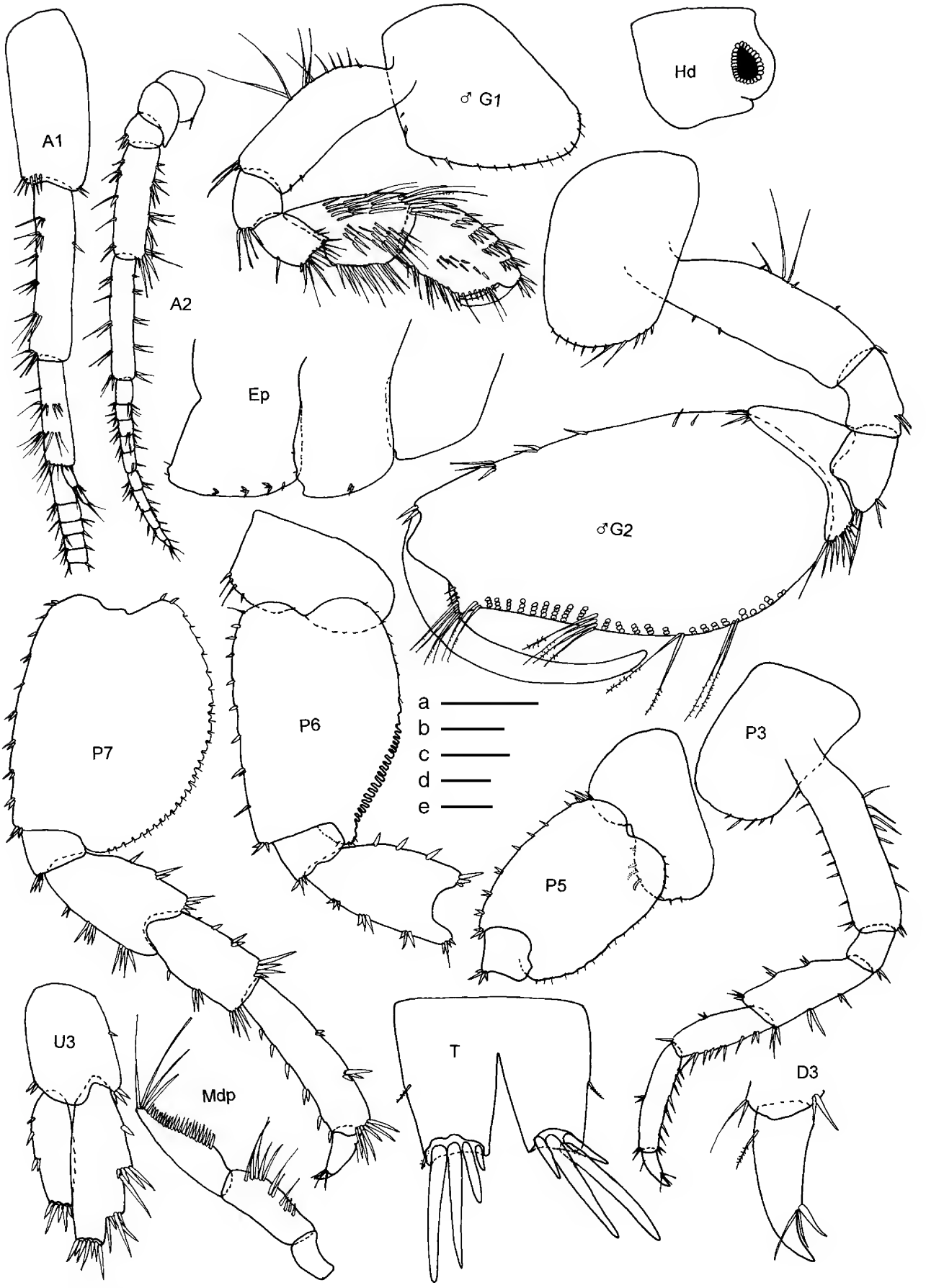

Fig. 4. *Elasmopus pectenicrus* (Bate): ♂, 6.2 mm, La Cuvette, scales *a* = 0.4 mm (*A1–2, P3, P5–7*), *b* = 0.2 mm (*G1–2*), *c* = 0.4 mm (*Hd, Ep*), *d* = 0.1 mm (*Mdp, U3*), *e* = 0.05 mm (*D3, T*).

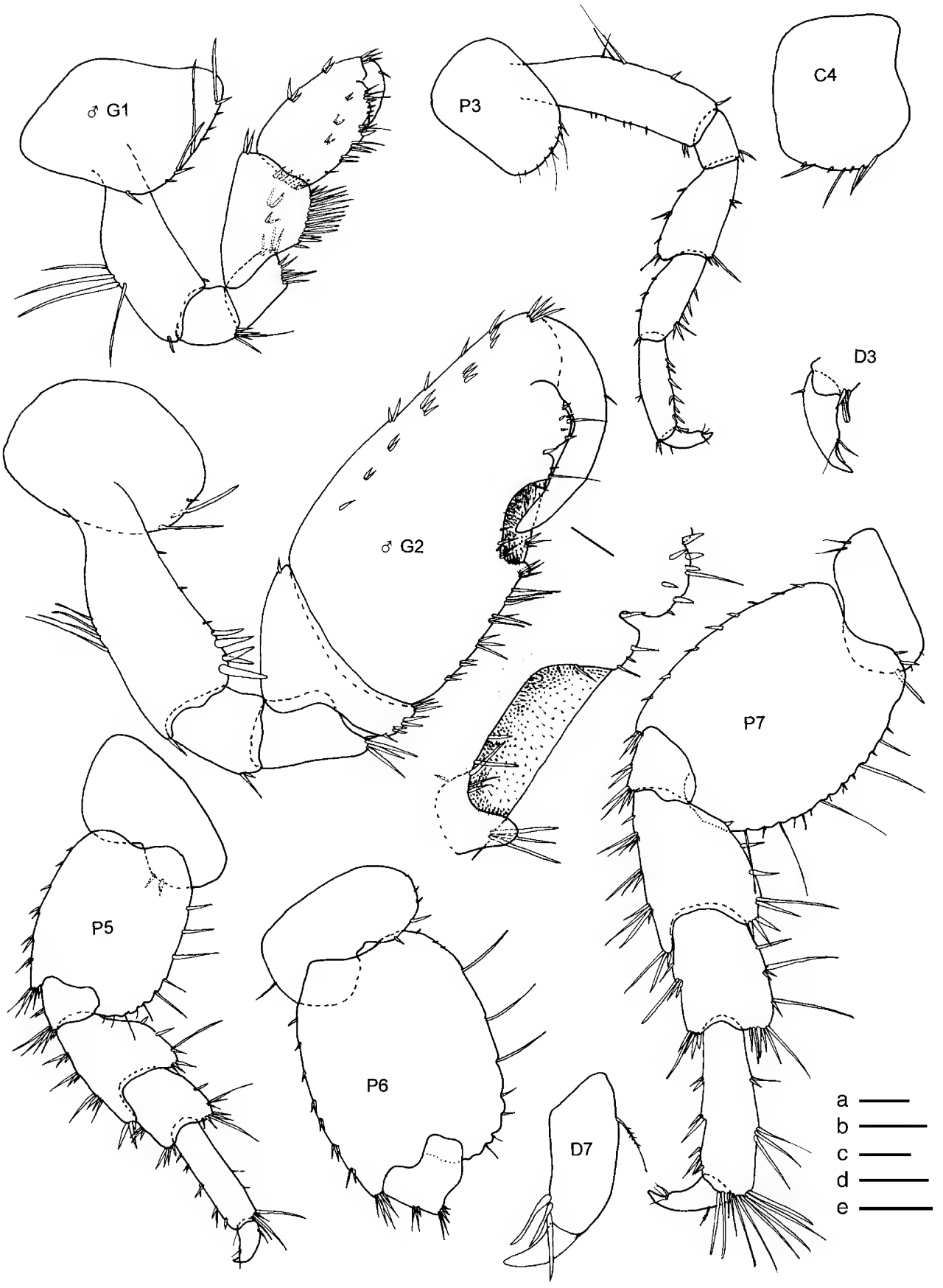

Fig. 5. *Elasmopus pseudinteger* n.sp.: ♂, 3.9 mm, Choisy, scales *a* = 0.1 mm (*G1–2*), *b* = 0.2 mm (*C4, P3*), *c* = 0.05 mm (*G2* enlargement, *D7*), *d* = 0.2 mm (*P5–7*), *e* = 0.1 mm (*D3*).

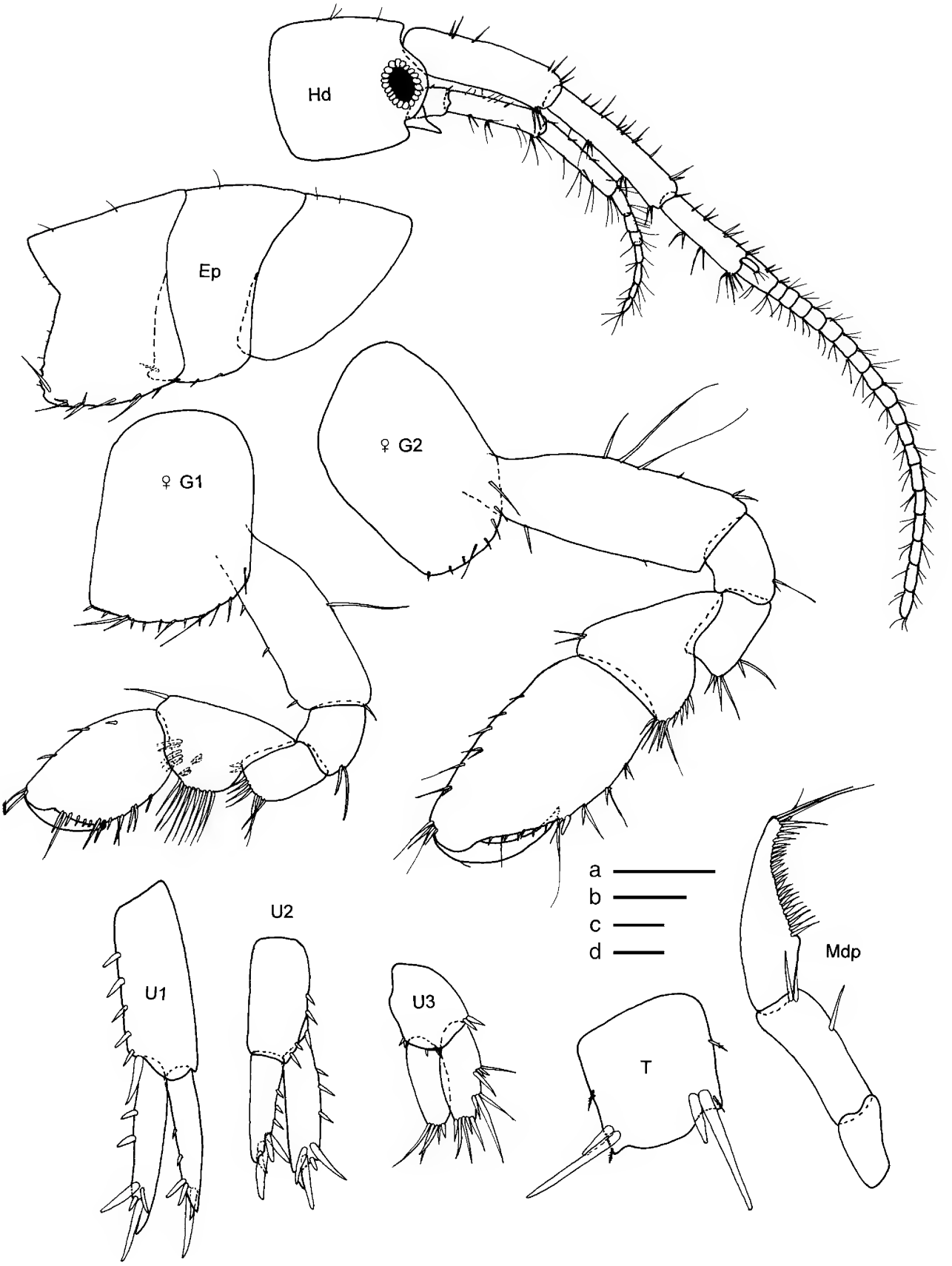

Fig. 6. *Elasmopus pseudinteger* n.sp.: ♂, 3.9 mm, Choisy, scales *a* = 0.4 mm (*Hd, Ep*), *c* = 0.1 mm (*U1–3*), *d* = 0.05 mm (*Mdp, T*); ♀, 3 mm, Anse la Raie, scale *b* = 0.1 mm (*G1–2*).

Elasmopus puteus n.sp.

Figs. 7, 8

Type material. HOLOTYPE: ♂, 2.8 mm, from mixture of the algae *Pocockiella variegata, Sargassum* sp., *Amphiroa* sp. and *Cymodocea* sp., Bain Boeuf (19°59'S 57°36'E), 16 Jun. 1999, AM P60546. PARATYPES: 1♂ and 3♀, same data as holotype, AM P60547; 1♂, 1♀ from the algae *Padina* sp., *Digenia simplex, Turbinaria ornata* and *Dictyota divaricata*, Roche Noires (20°6.2'S 57°44.5'E), 16 Dec. 1999, AM P60548.

Additional material examined. 2♂♂ from *Sargassum* sp. and *Turbinaria ornata*, Bain Boeuf, 15 May 1998. 1♂ from *Sargassum* sp., Roche Noires, 20 Jan. 1999. 8♂, 29♀, 9 juv., from mixture of the algae *Pocockiella variegata, Sargassum* sp., *Amphiroa* sp. and *Cymodocea* sp., Bain Boeuf, 16 Jun. 1999. 4♀ from mixture of *Sargassum* sp., *Turbinaria ornata* and *Pocockiella variegata*, Bain Boeuf, 12 Oct. 1999. 1♀ from mixture of *Padina* sp., *Pocockiella variegata* and coral rubble, Flic-en-Flac, 10 Dec. 1999. 1♂, 2♀ from *Padina* sp., *Digenia simplex, Turbinaria ornata* and *Dictyota divaricata*, Roche Noires, 16 Dec. 1999. 1♂, 1♀ from mixture of the algae *Padina* sp., *Turbinaria* sp., *Sargassum* sp., *Digenia* sp. and *Pocockiella variegata*, Bain Boeuf, 24 Jan. 2000. 2♀ from mixture of the algae *Sargassum* sp., *Digenia simplex, Centroceras clavulatum* and *Ulva reticulata*, La Cuvette (20°00'S 57°34.2'E), 25 Jan. 2000.

Description. Male: Length, 3 mm. Head, with subocular notch; eyes, small subround, with clear ommatidia. Antenna 1, peduncle articles sparsely setiferous; peduncle article 2, 0.6× article 1; article 3, 0.5× article 1; accessory flagellum 1-articulate; primary flagellum 13-articulate. Antenna 2, peduncle poorly setiferous; article 5, 0.9× article 4; flagellum 6-articulate, the terminal article rudimentary. Mandible, palp article 2 longest, with 1 medial and 2 distal setae; article 3 falcate, 0.7× article 2, with comb row of setae and 2 long terminal setae. Maxilla 1, inner plate with 2 terminal plumose setae. Labium, mandibular lobes rounded; outer plate with a blunt stout seta on inner margin. Maxilliped, palp article 3 with a small distal protuberance. Gnathopod 1, coxa produced distally, 1.5× as long as broad, with very short setae on distal margin; basis 2.3× as long as broad, posterior margin with a group of long setae; carpus and propodus subequal and each with long setae on the inner face of the anterior margin; propodus with palm almost transverse with a stout defining robust setae. Gnathopod 2, coxa 1.6× as long as broad, distal margin with very short setae; basis 3.2× as long as broad; carpus cup-shaped, twice as broad as long; propodus slender, subpyriform, twice as long as broad, 4× the length of carpus, palm oblique, posterior margin poorly setiferous, with a small subtriangular process on the inner subdistal face and a medial excavation forming a pit into which fits the tip of the dactylus; dactylus evenly curved, about half length of propodus. Pereopods 3–4, basis 3.3× as long as broad; propodus subequal to carpus; dactylus subdistally constricted. Pereopod 5, basis subquadrate tapering distally, posterior margin weakly crenulate with short setae. Pereopod 6, basis subquadrate, posterior margin weakly convex, crenulate and with short setae. Pereopod 7, basis strongly expanded, posterior margin very convex, crenulate with small setae. Epimeron 1 rounded. Epimera 2–3, produced into a weak posterodistal tooth and with a row of robust setae on the anterodistal margin. Uropod 1, rami subequal to each other and to peduncle. Uropod 2, peduncle 0.7× inner ramus; inner ramus 1.1× outer ramus. Uropod 3, peduncle subequal to inner ramus; inner ramus 0.8× outer ramus; inner ramus with lateral and terminal robust setae; outer ramus with lateral robust setae and a group of terminal robust setae and 1 long slender seta. Telson, deeply cleft; apices notched, outer tooth more developed than inner tooth, each with 1 long and 2 short robust setae.

Female secondary sexual characters: length, 2.5 mm (ovigerous). Gnathopod 1, similar to that of male but lacking long setae on the anterior margin of the carpus and propodus. Gnathopod 2, coxa 1.9× as long as broad; basis 3× as long as broad; carpus 1.4× as long as broad; propodus slender, 2.3× as long as broad, palm oblique, almost straight, defined by two robust setae; dactylus shorter than that of the male, overlapping the inner face of the propodus, but not fitting into a pit.

Remarks. In its general form this species resembles *Elasmopus gracilis* Schellenberg, 1938 but differs in the male gnathopod 2. The propodus posterior margin is sinuous (evenly convexin *E. gracilis*), lacks the dense setation of *E. gracilis* and has a distinct triangular process on the inner face, which is lacking in *E. gracilis*. In addition, the dactylus is much shorter than in *E. gracilis* and fits into a distinct pit.

This species can be distinguished from the other species of *Elasmopus* in Mauritius by the following combination of characters: its poorly setiferous antennae, coxae and propodus of gnathopod 2, and the largely expanded basis of pereopod 7 which is almost as broad as long. It is also a very small species.

Type locality. Bain Boeuf, Mauritius.

Distribution. Only known from Mauritius.

Etymology. From *puteus*—pit, referring to the pit on the inner face of the posterior margin of the male propodus into which fits the tip of the dactylus.

Elasmopus souillacensis n.sp.

Figs. 9, 10

Type material. HOLOTYPE: ♂, 3.5 mm, unique specimen, from mixture of *Amansia glomerata, Jania adherens* and *Sargassum densifolium*, Souillac (20°31'S 57°30.7'E), 10 Feb. 2000, AM P60549.

Description. Male, 3.5 mm. Head, with subocular notch; eyes subround with clear ommatidia. Antenna 1, moderately setiferous; peduncle article 2, 0.7× article 1; article 3, 0.5× article 1; accessory flagellum 2-articulate; primary flagellum 13-articulate. Antenna 2, moderately setiferous, article 5, 0.9× article 4; flagellum 7-articulate. Mandible, palp article 2 twice as long as article 1, with 1 medial seta and 2 distal setae; article 3 falcate, 1.1× article 2, with comb row of setae and 3 long apical setae. Maxilla 1, inner plate with 2 terminal plumose setae, and several fine setae on lateral margin. Labium, with mandibular lobes acute; outer plate with a blunt stout seta on inner margin. Maxilliped, palp article 3 with a small distal protuberance. Gnathopod 1, coxa 1.2× as long as broad, anterodistal margin slightly produced, distal margin with short setae about 0.2× the length of coxa; basis 2.6× as long as broad; carpus subequal to propodus; propodus with few groups of setae on medial face, palm defined by a robust seta. Gnathopod 2, coxa

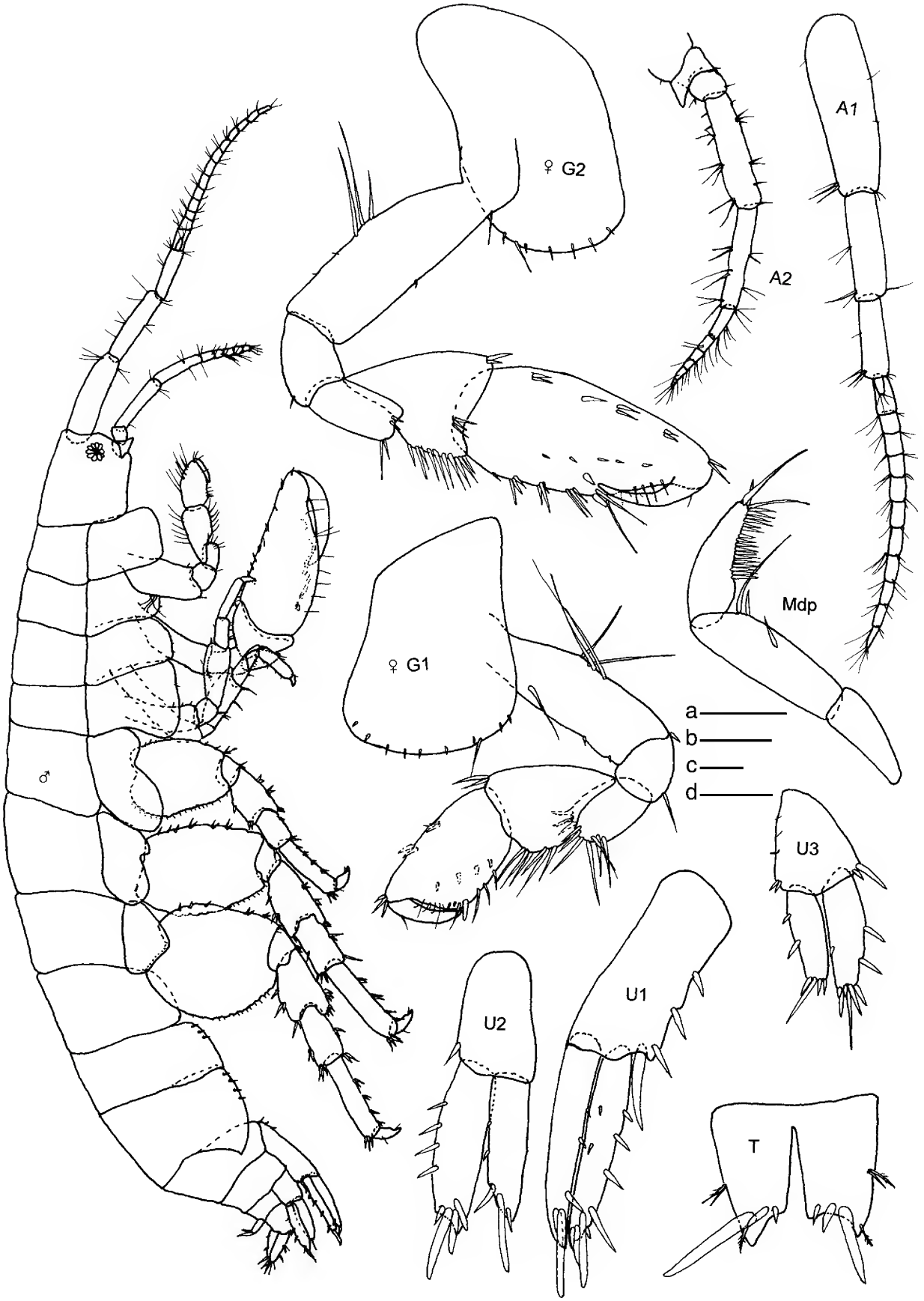

Fig. 7. *Elasmopus puteus* n.sp.: ♂, 3 mm, Bain Boeuf, scales *a* = 0.4 mm (whole animal), *b* = 0.1 mm (*U1–3*), *c* = 0.1 mm (*A1–2*), *d* = 0.05 mm (*Mdp, T*); ♀, 2.5 mm, Bain Boeuf, scale *b* = 0.1 mm (*G1–2*).

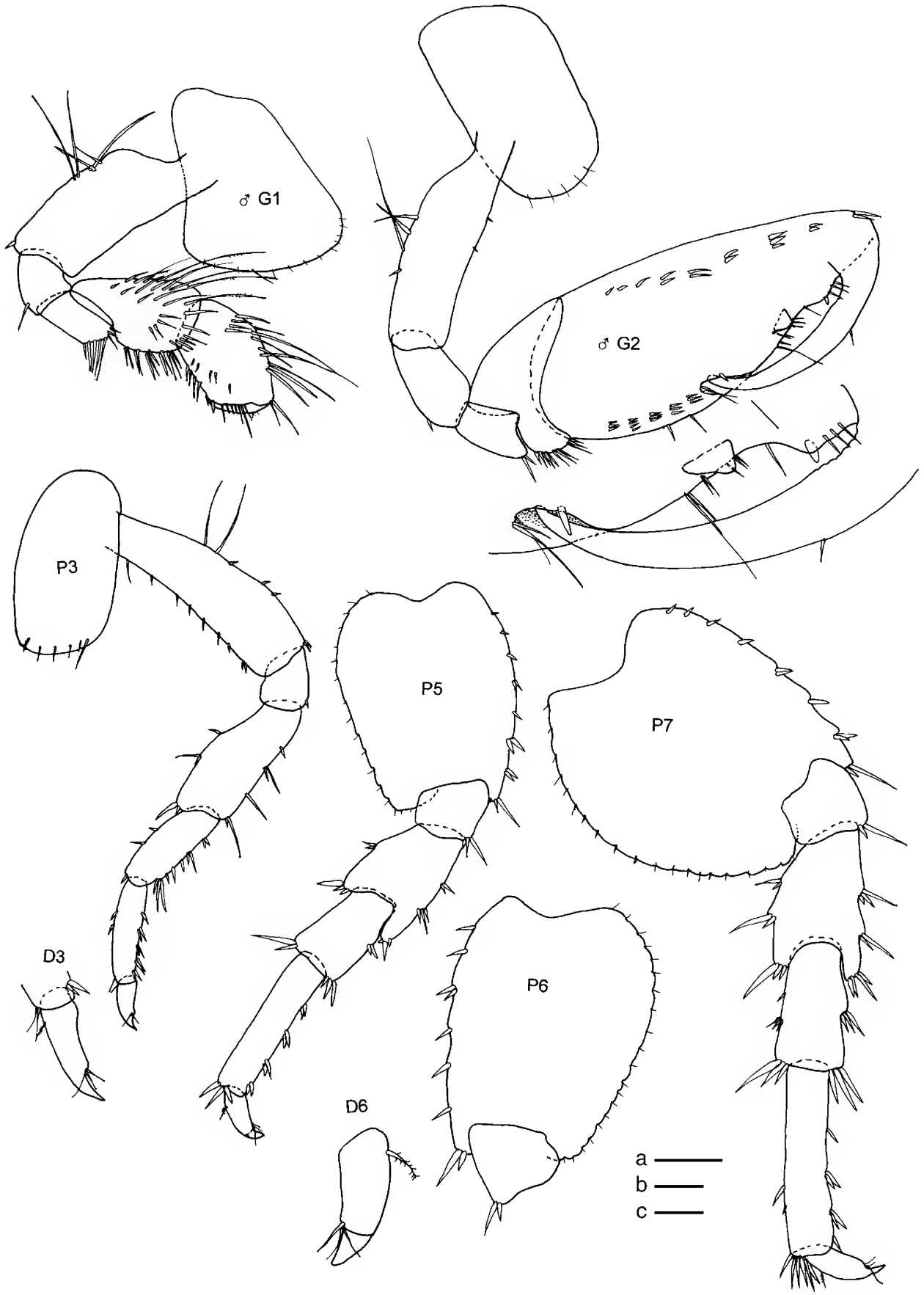

Fig. 8. *Elasmopus puteus* n.sp.: ♂, 3 mm, Bain Boeuf, scales *a* = 0.2 mm (*G1*), *b* = 0.1 mm (*G2, P3, P5–7*), *c* = 0.05 mm (*D3, D6*, enlargement of *G2*).

1.2× as long as broad, distal margin with short setae and a few long setae about one-third length of coxa; basis 2.5× as long as broad; carpus reduced, cup-shaped, 2.2× as broad as long; propodus 2.1× as long as broad, narrowing distally, posterior margin moderately setiferous, with a medial rounded process and a short, oblique palm; dactylus robust, medially expanded and about two-thirds length of propodus. Pereopods 3–4, coxa 1.8× as long as broad; basis 3.6× as long as broad; propodus posterodistal margin with 1 striate sabre seta and 1 normal robust seta; dactylus distally constricted. Pereopods 5–6, basis subquadrate, posterior margin almost straight, weakly crenulate and with short setae. Pereopod 7, basis subovoid, posterior margin weakly crenulate with short setae. Epimera 1–2, posterodistal margin produced into a weak tooth. Epimeron 3, subquadrate with a row of robust setae on the anterodistal margin. Uropod 1, peduncle 1.4× inner ramus; outer ramus 0.9× inner ramus. Uropod 2, peduncle subequal to outer ramus; outer ramus 0.9× inner ramus. Uropod 3, peduncle 0.8× rami; inner and outer rami subequal; inner ramus with robust setae on lateral margin and an apical bunch of robust setae and 1 slender seta; outer ramus with 3 groups of robust setae on the lateral margin and several robust and 2 long fine apical setae. Telson, tapered, cleft to 75% its length; lobes notched with outer tooth more produced than inner tooth; each lobe with 2 strong apical robust setae.

Female. Unknown.

Remarks. *Elasmopus souillacensis* differs from all other species of *Elasmopus* by the combination of: short setae on coxae 1 and 2, the shape of the male gnathopod 2, the subequal rami of uropod 3 and the tapered and notched telson.

Type locality. Souillac, Mauritius.

Distribution. Mauritius.

Etymology. The specimen is named after the type locality.

Elasmopus spinidactylus Chevreux

Fig. 11

Elasmopus spinidactylus Chevreux, 1908: 486, figs. 9, 10.–Walker, 1909: 336.–Schellenberg, 1938: 55.–Shoemaker, 1942: 13.–J.L. Barnard, 1965: 504.–J.L. Barnard, 1970: 136, figs. 81, 82.–Sivaprakasam, 1966: 104, fig. 8; 1968: 50, fig. 6g,h.–Ledoyer, 1972: 223, pl. 40.–Ledoyer, 1982: 482, fig. 183.–Myers, 1985: 108, fig. 86.–Appadoo & Steele, 1998: 639.

Material examined. 2♂♂, 8♀♀, 6 juv., from the alga *Acanthophora spicifera*, Souillac (20°31'S 57°30.7'E), 3 Feb. 1998. 5♂♂, 9♀, 3 juv., from a mixture of the algae *Acanthophora spicifera, Amansia glomerata* and *Boodlea* sp., Souillac, 13 Aug. 1998. 2♂♂, 8♀, 2 juv., from mixture of the algae *Gracilaria millardetii, Centroceras clavulatum, Digenia simplex* and *Acanthophora spicifera*, Souillac, 10 Nov. 1998. 1♂, 1♀ from *Acanthophora spicifera*, Souillac, 25 Mar. 1999. 2♂♂, 3♀ from *Acanthophora spicifera* and *Centroceras clavulatum*, Souillac, 8 Apr. 1999. 1♂ from mixture of the algae *Sargassum* sp., *Ulva lactuca* and *Acanthophora spicifera*, Souillac, 14 Oct. 1999. 1♀ from mixture of *Digenia simplex* and *Sargassum densifolium*, Rivière des Galets (20°30'S 57°27'E), 16 Nov. 1999. 1♂, 1♀, 5 juv., from a mixture of *Amansia glomerata, Gracilaria millardetii, Sargassum* sp., Souillac, 14 Dec. 1999. 1♀, from a mixture of *Digenia simplex, Centroceras clavulatum, Sargassum* sp., La Cuvette (20°00'S 57°34.2'E), 25 Jan. 2000. 1♂, 3♀, 2 juv., from a mixture of the algae *Amansia glomerata, Jania adherens* and *Sargassum densifolium*, Souillac, 10 Feb. 2000.

Description. Male: length, 5.2 mm. Head, with subocular notch; eyes large, oval with well-developed ommatidia. Antenna 1, moderately setiferous; article 2, 0.7× length article 1; article 3, 0.6× length of article 1; accessory flagellum 2-articulate; primary flagellum 16-articulate. Antenna 2, peduncle articles with long setae; article 5, slightly shorter than article 4; flagellum 7-articulate. Mandible palp article 2 with 1 medial seta and 4 long distal setae; article 3 falcate, 1.2× length of article 2, with comb-row of setae and 3 long apical setae. Maxilla 1, inner plate with 2 terminal plumose setae and several fine setae on inner margin. Labium, with mandibular lobes acute; outer plate with blunt stout seta on inner margin. Maxilliped, palp article 3 with small protuberance at distal end. Gnathopod 1, coxa subquadrate, 0.8× as long as broad, distal margin with a patch of setae, the longest seta 0.7× length of coxa; basis 2.2× as long as broad with 1 seta on posterior margin; carpus 0.9× length of propodus; propodus 1.6× as long as broad, with two semicircular comb-rows of setae on inner face; palm defined by a short, stout, robust seta. Gnathopod 2, coxa subquadrate, about as long as broad; basis twice as long as broad; carpus reduced, 3.5× as broad as long; propodus 8× as long as carpus, 1.8× as long as broad, posterior margin strongly setose, produced distally into an outwardly deflected flat-topped, obtuse process, palm with a few stout robust setae and long slender setae; dactylus 0.7× length of propodus. Pereopod 3–4, propodus posterodistal margin with 1 large striate, sabre, locking seta and 1 normal robust seta; dactylus with small nipple-like processes and subdistally constricted. Pereopods 5–7, dactylus posterior margin with nipple-like processes Pereopod 5, basis subovoid. Pereopod 6, basis subquadrangular and produced posterodistally into a triangular lobe; Pereopod 7, basis posterior margin convex with short setae. Epimera 1–3, with weak posterodistal tooth. Uropod 1, peduncle 1.2× length of inner ramus; rami subequal. Uropod 2, peduncle shorter than inner ramus; outer ramus 0.8× inner ramus. Uropod 3, peduncle subequal to outer ramus; inner ramus three-quarter length of outer ramus; inner ramus with terminal robust seta, outer ramus with lateral and terminal robust setae. Telson, short, cleft to 50% its length, apices broad and truncate with 2 robust setae on each lobe.

Female secondary sexual characters: length, 5.2 mm (ovigerous). Gnathopod 1, coxa 1.2× as long as broad, distal margin with a patch of long setae about half length of coxa; other features similar to those of male gnathopod 1. Gnathopod 2, coxa subquadrate as long as broad; basis 2.7× as long as broad with 1 seta on posterior margin; carpus 1.5× as broad as long; propodus 1.8× as long as broad, similar to that of male but lacking posterodistal process, palm oblique, with short robust setae, distal margin densely setose; dactylus 0.7× length of propodus.

Remarks. Both males and females of *Elasmopus spinidactylus* are easily recognized by the nipple-like processes on the dactylus of P3–7. The females of this species have an enlarged propodus similar to that of the male.

Habitat. This species occurs mostly on red algae in Mauritius.

Type locality. Makapou Island, Gambier Archipelago.

Distribution. Madagascar, Mauritius, Chagos Archipelago, India, Fiji, Micronesia, Melanesia, Polynesia, Hawaii, Venezuela.

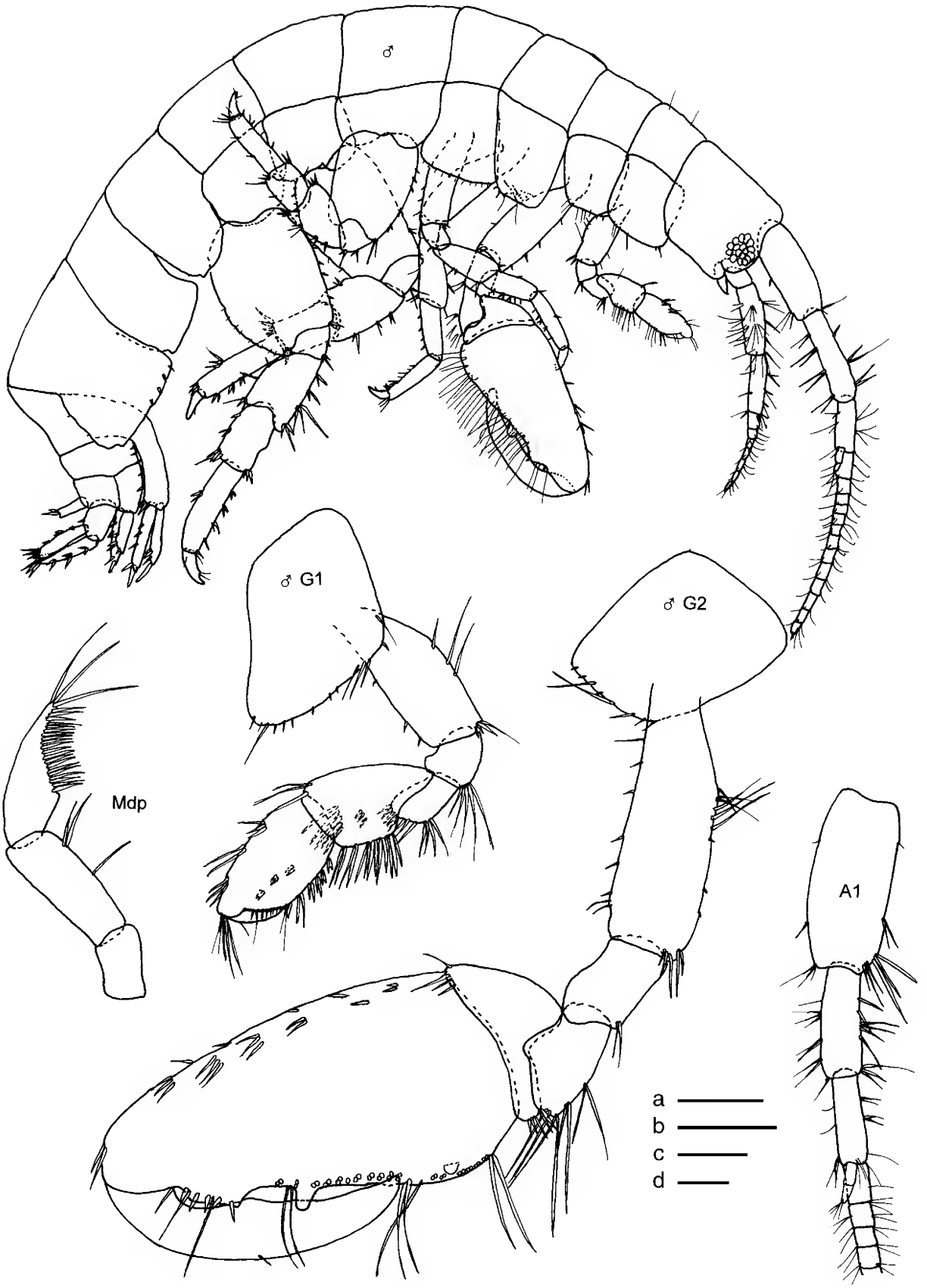

Fig. 9. *Elasmopus souillacensis* n.sp.: ♂, 3.5 mm, Souillac, scales *a* = 0.4 mm (whole animal), *b* = 0.2 mm (*G1–2*), *c* = 0.2 mm (*A1*), *d* = 0.05 mm (*Mdp*).

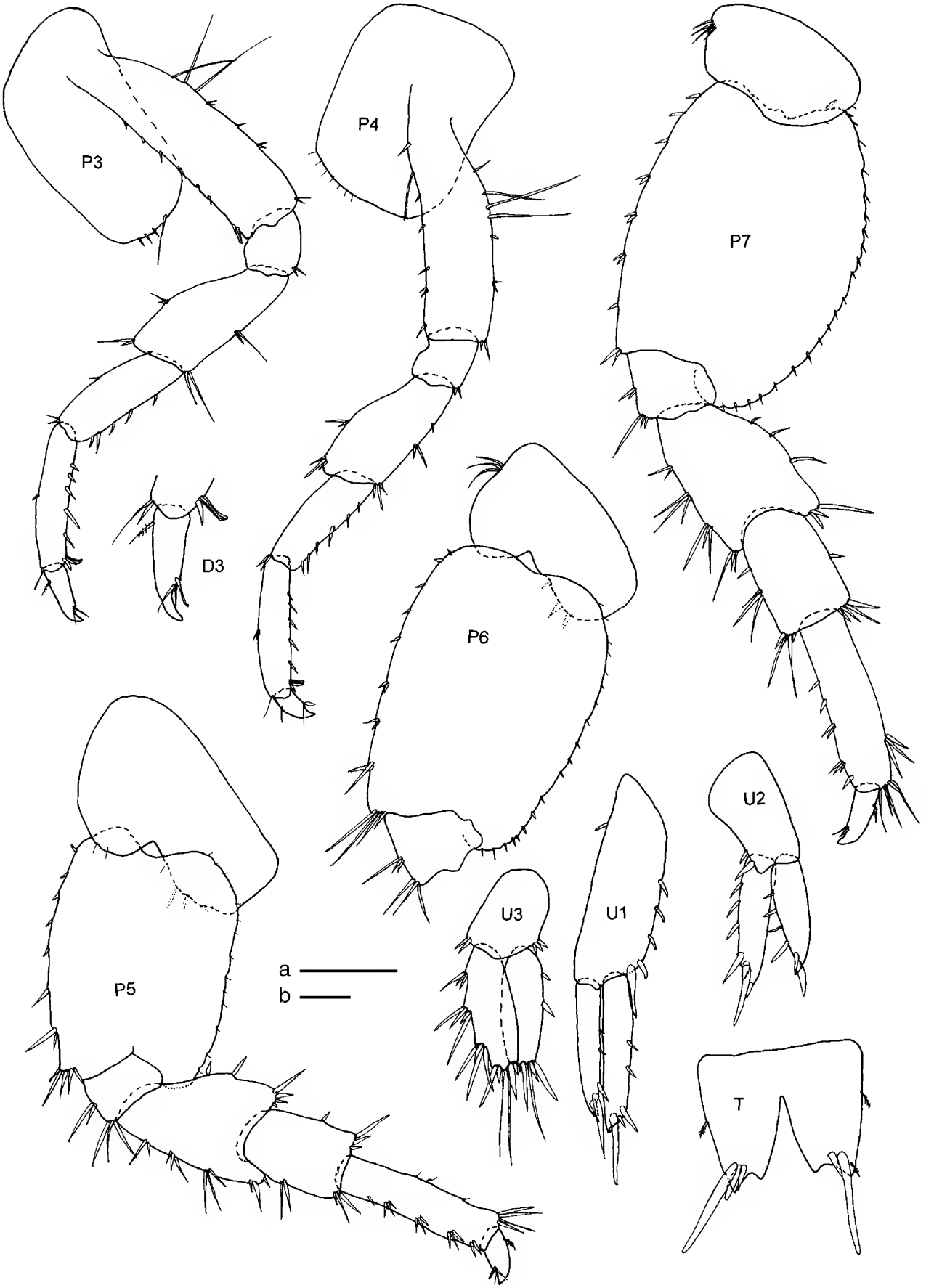

Fig. 10. *Elasmopus souillacensis* n.sp.: ♂, 3.5 mm, Souillac, scales *a* = 0.2 mm (*P3–7, U1–3*), *b* = 0.05 mm (*D3, T*).

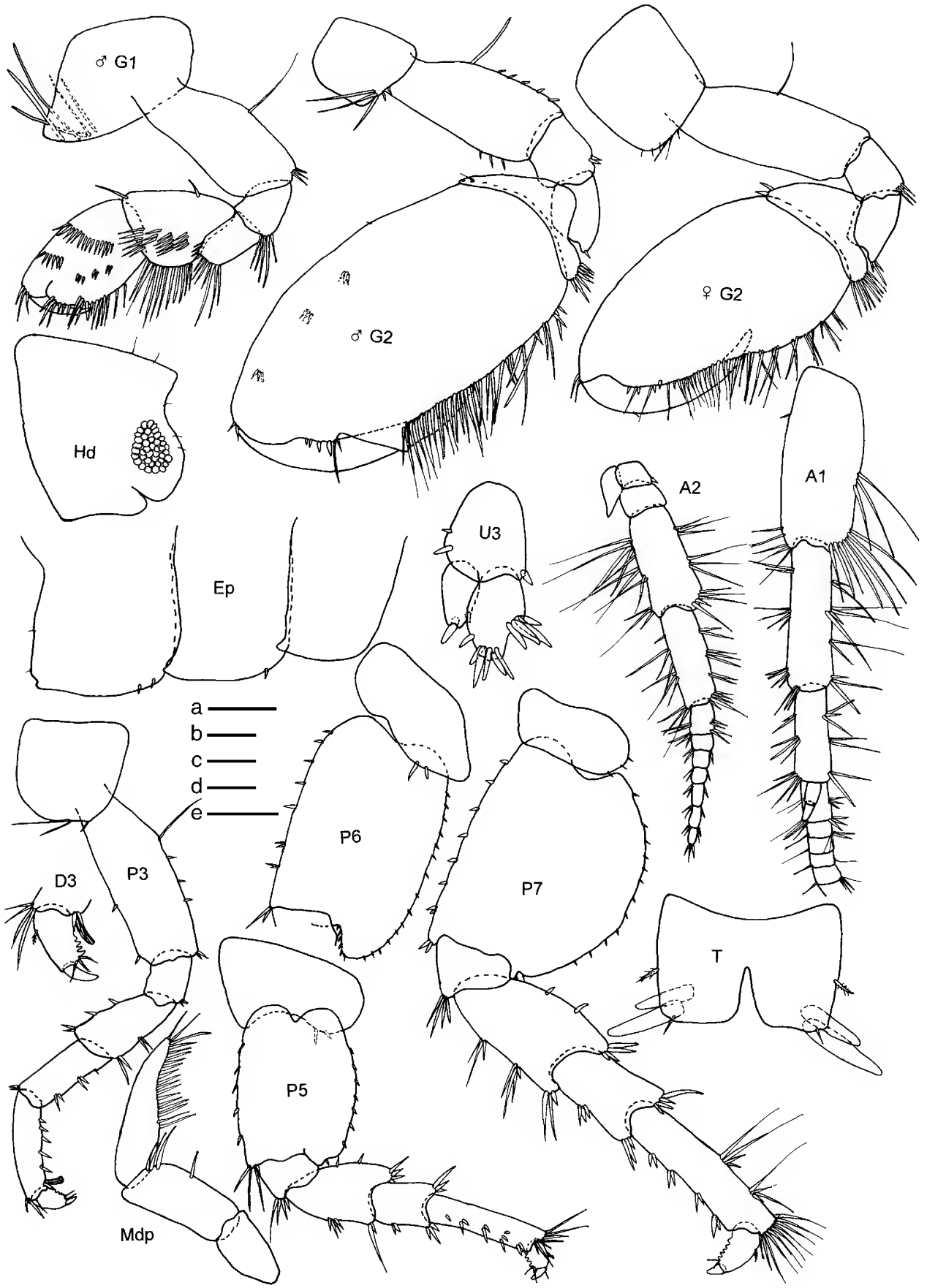

Fig. 11. *Elasmopus spinidactylus* Chevreux: ♂, 5.2 mm, Souillac, scales *a* = 0.2 mm (G1), *b* = 0.2 mm (*Hd, A1–2, G2, P3–7, Ep*), *c* = 0.1 mm (*D3, U3*), *d* = 0.05 mm (*T*), *e* = 0.1 mm (*Mdp*); ♀, 5.2 mm, Souillac, scale *a* = 0.2 mm (*G2*).

Elasmopus spinimanus Walker

Fig. 12

Elasmopus spinimanus Walker, 1904: 277, pl. 5, fig. 36.–Pirlot, 1936: 313.–Schellenberg, 1938: 55.–Myers, 1985: 109, fig. 87.

Material examined. 1♂, from mixture of *Amansia glomerata, Jania adherens* and *Sargassum densifolium*, Souillac (20°31'S 57°30.7'E), 10 Feb. 2000.

Description. Male, 3.8 mm. Head, with subocular notch; eyes large, subround with circular disc of clear ommatidia enclosing a dark core. Antenna 1, article 2 subequal to 1; article 3, 0.5× article 1; accessory flagellum 3-articulate, article 3 vestigial; primary flagellum 20-articulate. Antenna 2, article 5, 0.8× article 4; flagellum 7-articulate, the terminal article rudimentary. Mandible, palp article 2 with 1 strong distal seta and 2 short medial setae; article 3 falcate, 1.1× article 2 with a comb row of setae and 3 long terminal setae. Maxilla 1, inner plate with 2 terminal plumose setae, and several fine setae on inner margin. Labium, with mandibular lobes acute; outer plate with 2 stout setae. Maxilliped, palp article 3 with a small distal protuberance. Gnathopod 1, coxa 1.4× as long as broad, anterodistal corner slightly produced, distal margin with short setae; basis 2.5× as long as broad; propodus 1.4× carpus with 2 semicircular rows of setae on anterior margin, palm defined by a robust seta. Gnathopod 2, coxa 1.6× as long as broad with short setae on distal margin; basis slender, 4× as long as broad; carpus cup-shaped, 1.5× as broad as long; propodus 2.2× as long as broad and 3.6× length of carpus, posterior margin poorly setiferous, palm sinuous, palm and posterodistal margin with strong stout robust setae; dactylus curved and about half length of propodus. Pereopod 3–4, propodus posterodistal margin with 1 striate, sabre seta and 1 short, straight, robust seta; dactylus constricted subdistally at the junction of the unguis. Pereopod 5, basis subovoid, posterior margin weakly crenulate with short robust setae. Pereopod 6, basis, posterior margin weakly convex, weakly serrated with short setae. Pereopod 7, basis posterior margin weakly convex, serrated and with short setae. Epimera 1–3, posterodistal margin produced into a small but distinct tooth. Epimera 2–3, with robust setae on the anterodistal margin. Uropod 1, peduncle 1.3× inner ramus; outer ramus 0.8× inner ramus. Uropod 2, peduncle subequal to outer ramus; outer ramus 0.8× inner ramus. Uropod 3, peduncle 0.6× outer ramus; rami subequal with robust setae on margins and apices. Telson, cleft to about 80% its length, lobes tapered, notched at tip with an acute inner tooth, each lobe with 2 robust setae.

Remarks. The present material agrees well with Walker's description of *Elasmopus spinimanus*, except that the male gnathopod 2 propodus is subquadrate proximally and excavate on the posterodistal margin (subpyriform in Walker's material). The present material also closely resembles the material described by Myers (1985) from Fiji except that in that material, the coxae of gnathopods 1 and 2 have longer setae, the excavation on the palm of the male gnathopod 2 is not well developed and the telson has more setae on the lateral margins. Fijian material examined in the present work, has the posterodistal margins of the propodus of pereopods 3 and 4 with 1 striate locking seta and 1 normal robust seta (c.f. Myers, 1985, fig. 87). The tapered and notched telson, the subequal uropods 3 and the spinous, poorly setiferous palm of gnathopod 2 taken together, distinguish this species from other *Elasmopus* from Mauritius.

Type locality. Sri Lanka.

Distribution. Mauritius, Sri Lanka, Fiji.

Elasmopus steelei n.sp.

Figs. 13, 14

Elasmopus sp. 1.–Appadoo & Steele, 1998: 639.

Type material. HOLOTYPE: ♂, 3.3 mm from mixture of the algae *Sargassum densifolium, Amansia glomerata, Jania adherens* and *Digenia simplex*, Souillac (20°31'S 57°30.7'E), 14 Oct. 1999, AM P60550. PARATYPES: 3♂♂, 1♀, same data as holotype, AM P60551; 3♂♂, 7♀ from *Sargassum densifolium* and *Amansia glomerata*, Souillac, 4 Aug. 1999, AM P60552.

Material examined. 4♂♂, 4♀♀, 3 juv., from *Sargassum densifolium* and *Ulva reticulata*, Souillac, 3 Feb. 1998. 1♂ from the alga *Gelidiella* sp., Flic-en-Flac, opposite Klondike Hotel (20°15.7'S 57°22'E), 12 May 1998. 2♂♂, from the algae *Amansia glomerata* and *Boodlea* sp., Souillac, 13 Aug. 1998. 2♂♂, 2♀, from the alga *Dictyota divaricata*, La Cuvette, 28 Aug. 1998. 15♂♂, 15♀, 6 juv., from the algae *Amansia glomerata, Ulva reticulata, Acanthophora spicifera*, Souillac, 25 Mar. 1999. 1♂, 1♀ from *Sargassum* sp. and *Ulva reticulata*, La Cuvette (20°00'S 57°34.2'E), 5 May 1999. 1♂, 8♀, 5 juv., from *Sargassum densifolium* and *Amansia glomerata*, Souillac, 4 Aug. 1999. 5♂♂, 2♀, 3 juv., from mixture of *Sargassum densifolium, Amansia glomerata, Jania adherens* and *Digenia simplex*, Souillac, 14 Oct. 1999. 4♂♂, 3♀, 4 juv., from mixture of *Sargassum densifolium, Ulva reticulata, Amansia glomerata* and *Jania adherens*, Souillac, 10 Feb. 2000.

Description. Male: length, 2.8 mm. Head, with subocular notch; eyes small and round. Antenna 1, densely setose; peduncle articles 1 and 2 subequal; article 3, 0.6× article 1; accessory flagellum 2-articulate, the terminal article vestigial; primary flagellum 20-articulate. Antenna 2, densely setose; article 5, 0.9× article 4; flagellum 9-articulate. Mandible palp, article 2, 1.4× article 1, with 1 medial and 2 distal setae; article 3 falcate, 1.1× article 2, with a comb row of setae and 2 long apical setae. Maxilla 1, inner plate with 2 plumose terminal setae and several fine marginal setae. Labium, with mandibular lobes acute; outer plate with a blunt stout seta on inner margin. Maxilliped, palp article 3 with a small distal protuberance. Gnathopod 1, coxa anterodistally produced, about as long as broad, distal margin densely setose, a few setae equal to the depth of the coxa; basis 2.4× as long as broad; carpus inner face densely setose, subequal in length to propodus; propodus inner face densely setose, palm defined by a robust seta. Gnathopod 2, coxa 1.2× as long as broad, distal margin with setae about half length of coxa; basis 2.6× as long as broad, anterodistal margin with stout robust setae; carpus cup-shaped, 1.8× as broad as long; propodus twice as long as broad, 4.5× length of carpus, posterior margin weakly sinuous and with dense rows of pectinate setae; dactylus elongate, nearly two thirds length of propodus, inner margin expanded at about a quarter its length. Pereopods 3–4, coxa distal margin with a strong group of setae about half length of coxa; basis 3× as long as broad; propodus posterodistal margin with 1 striate sabre seta and

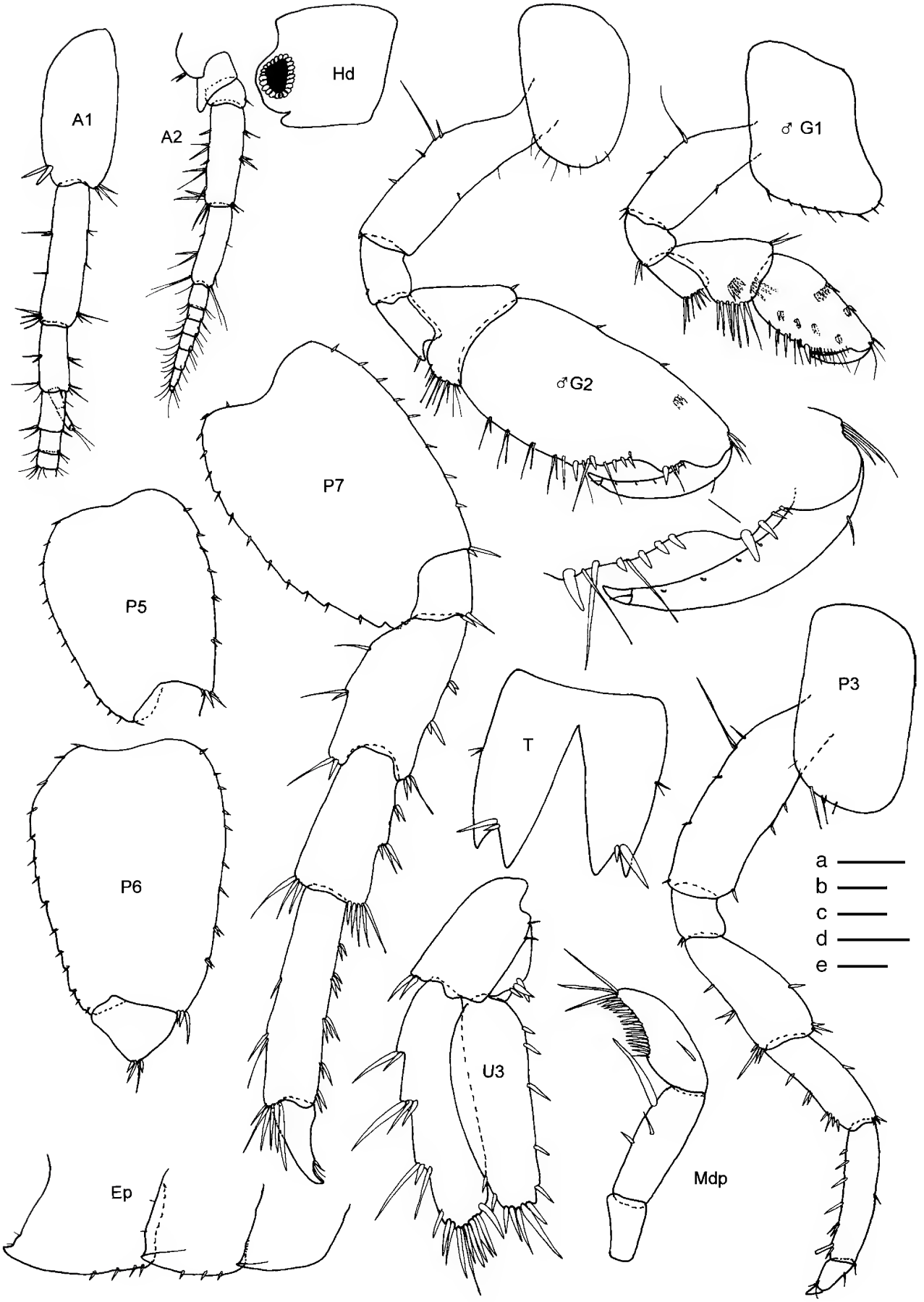

Fig. 12. *Elasmopus spinimanus* Walker: ♂, 3.8 mm, Souillac, scales *a* = 0.2 mm (*A1–2*), *b* = 0.2 mm (*Hd, Ep*), *c* = 0.1 mm (*G1–2, P3, P5–7*), *d* = 0.1 mm (*U3, T*), *e* = 0.05 mm (*Mdp*, enlargement of *G2*).

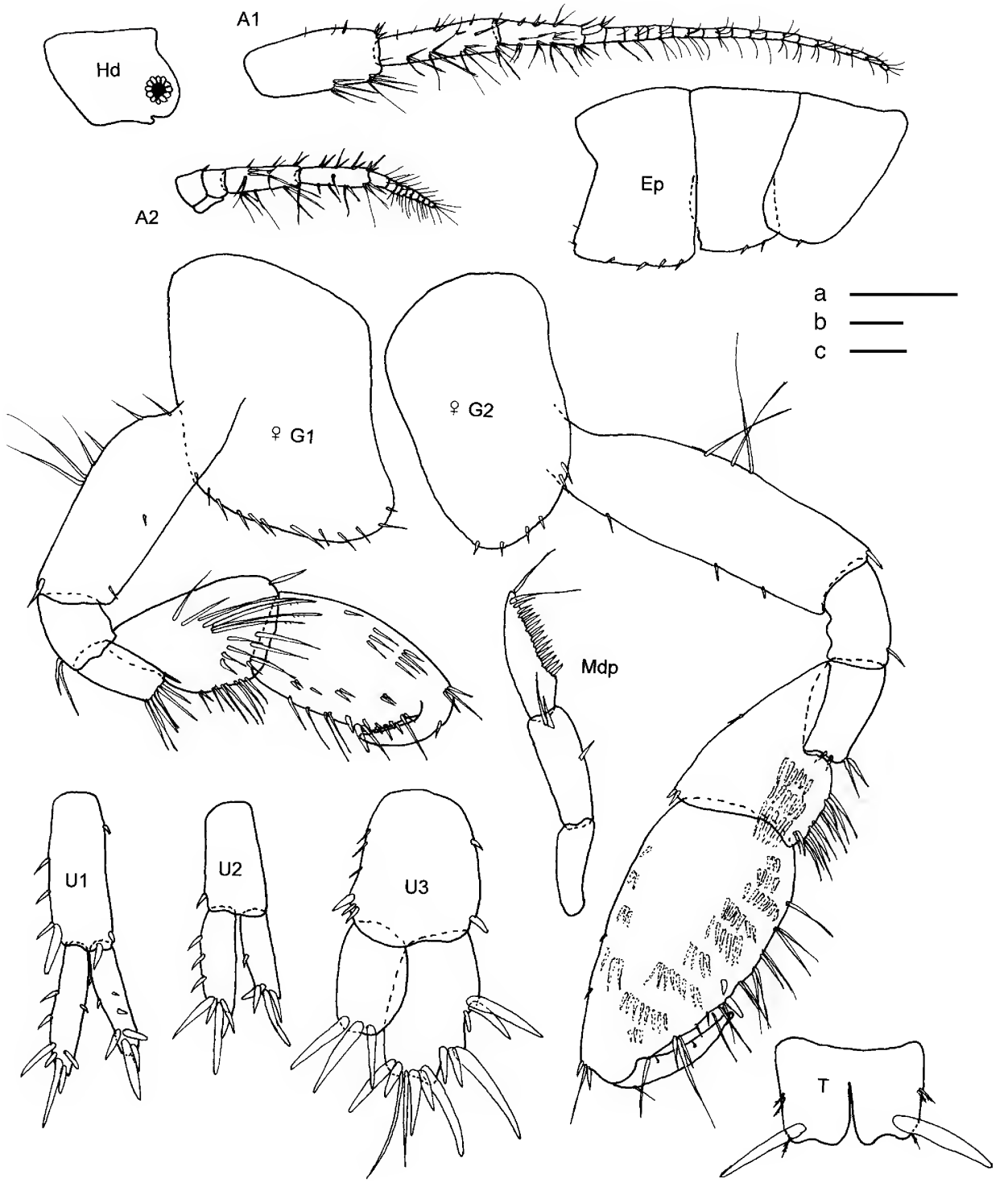

Fig. 13. *Elasmopus steelei* n.sp.: ♂, 2.8 mm, Souillac, scales *a* = 0.4 mm (*A1–2, Hd, Ep*), *b* = 0.1 mm (*U1–2*), *c* = 0.05 mm (*Mdp, T, U3*); ♀, 2.3 mm, Souillac, scale *c* = 0.05 mm (*G1–2*).

1 normal robust seta; dactylus subdistally constricted. Pereopod 5, basis subquadrangular, posterior margin weakly crenulate and with short setae. Pereopod 6, basis subquadrangular, posterior margin weakly concave, weakly crenulate with short setae. Pereopod 7, basis subovate, posterior margin strongly convex, castelloserrate with short setae. Epimera 1–3, with a row of robust setae on anterodistal margin. Epimeron 1, subquadrate. Epimeron 2, slightly produced into a weak posterodistal tooth. Epimeron 3, subquadrate. Uropod 1, peduncle 1.3× rami; rami subequal. Uropod 2, peduncle subequal to outer ramus; outer ramus 0.8× inner ramus. Uropod 3, inner ramus 0.8× outer ramus and with terminal robust setae only; outer ramus 0.9× peduncle, with two groups of robust setae on the lateral margins and a group of robust and 2 slender apical setae. Telson, cleft to 75% its length; lobes notched, each lobe with 1 strong robust seta.

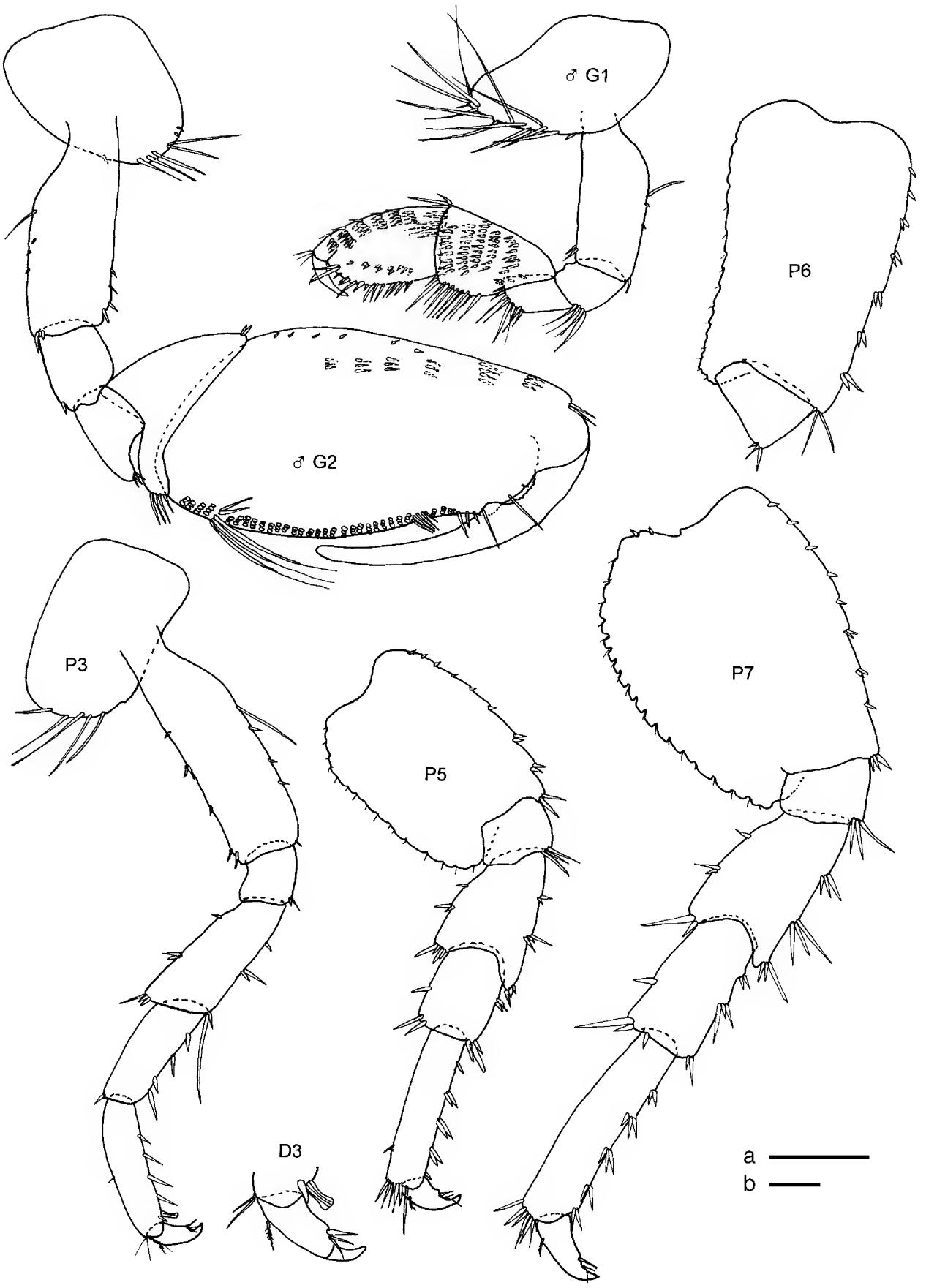

Fig. 14. *Elasmopus steelei* n.sp.: ♂, 2.8 mm, Souillac, scales *a* = 0.2 mm (*G1–2, P3, P5–7*), *b* = 0.05 mm (*D3*).

Variation with size. In younger males the robust setae on the distal end of the basis of gnathopod 2 are not well developed, the dactylus of gnathopod 2 is shorter and the medial expansion of the dactylus is weak.

Female secondary sexual characters: length, 2.3 mm (ovigerous). Gnathopod 1, coxa 1.3× as long as broad, distal margin with numerous short setae; basis 2.6× as long as broad; propodus 1.2× length of carpus, 1.9× as long as broad, palmar margin with a defining robust seta. Gnathopod 2, coxa 1.5× as long as broad; basis 3× as long as broad; carpus 1.5× as long as broad; propodus 2.1× as long as broad, palm defined by a stout robust seta; dactylus fitting palm.

Remarks. This species is superficially similar to *E. ecuadorensis* Schellenberg (see also J.L. Barnard, 1979), but differs in several ways. The male gnathopod 2 coxa bears long setae and the basis anterodistal margin has robust setae, both characters absent in *E. ecuadorensis* and the propodus has a weakly developed palmar protrusion (strongly transverse in *ecuadorensis*). The propodus of pereopods 3–4 has a striate, sabre, locking seta (striate but lanceolate in *E. ecuadorensis*). The posterior margin of the basis of pereopod 6 is concave in present material but straight to weakly convex in *E. ecuadorensis* and pereopod 7 basis is castellate in present material but weakly serrate in *Elasmopus ecuadorensis*. *Elasmopus steelei* also resembles *E. lapu* Myers and *E. palu* n.sp., but differs from both species in several ways. In *E. steelei*, the male gnathopod 2 basis bears a row of robust setae on the anterodistal margin (absent in *E. lapu* and *E. palu*) and lacks the well-developed palmar shelf and the well-developed ridge which occurs on the inner face of the propodus of *E. lapu* and *E. palu*. In addition, the basis of pereopod 6 is more elongate and the posterior margin is concave. In addition, *E. steelei* differs from *E. palu* n.sp. in the long setae on the male coxa 1–2 and in the subquadrate epimeron 3 (two teeth in *E. palu*).

This species can be distinguished from other *Elasmopus* species from Mauritius by the following combination of characters: the densely setose distal margin of coxae, the densely setose posterior margin of male gnathopods 1 and 2; the medially expanded dactylus of the male gnathopod 2, the striate sabre seta on the propodus of pereopods 3 and 4 and the characteristically shaped basis of pereopod 6.

Type locality. Souillac, Mauritius.

Distribution. Mauritius.

Etymology. This species is named after Prof. Donald H. Steele of Memorial University of Newfoundland, in recognition for having introduced one of the authors (CA) to the study of amphipods.

Key to the species of *Elasmopus* recorded from Mauritius

1 Uropod 3 rami subequal in length 2
—— Uropod 3 rami unequal, inner ramus shorter than outer 4

2 Telson entire ..... (Figs. 5, 6) *E. pseudinteger*
—— Telson cleft 3

3 Telson with longest robust seta as long as telson; male G2, propodus pyriform, posterior margin with medial tooth; dactylus broad, two-thirds length of propodus ..... (Figs. 9, 10) *E. souillacensis*
—— Telson with longest robust seta less than a quarter length of telson; male G2 propodus subquadrangular posterior margin without medial tooth, dactylus relatively slender, half length of propodus ..... (Fig. 12) *E. spinimanus*

4 Pereopods 3–4 propodus posterodistal margin with striate sabre shaped robust seta 5
—— Pereopods 3–4 propodus posterodistal margin with straight robust setae only 8

5 Pereopods 3–7 dactylus posterior margin with small nipple-like projections ..... (Fig. 11) *E. spinidactylus*
—— Pereopods 3–7 dactylus without nipple-like projections 6

6 Gnathopod 2 male basis anterior margin with dense brush of long setae, propodus with two teeth on posterior margin ..... *E. molokai pilosus*
—— Gnathopod 2 male basis anterior margin without dense brush of long setae, propodus posterior margin lacking teeth 7

7 Epimeron 3, posterodistal margin without teeth, male coxae 1–2 with some setae as long as coxa ..... (Figs. 13, 14) *E. steelei*

—— Epimeron 3, posterodistal margin with two small teeth, male coxae 1–2 with setae much shorter than length of coxae ..... (Fig. 3) *E. palu*

8 Pereopod 6–7, basis deeply castelloserrate ..... (Fig. 4) *E. pectenicrus*

—— Pereopod 6–7, basis weakly serrated 9

9 Gnathopod 2, male propodus posterior margin densely setose ..... (Figs. 1, 2) *E. menurte*

—— Gnathopod 2, male propodus posterior margin only weakly setiferous 10

10 Coxa 1–2 male with some long setae on distal margin 11

—— Coxa 1–2 male with short setae only 12

11 Coxa 1 male anterodistal corner acute, P7 basis distinctly longer than broad ..... *E. pseudaffinis* form B Ledoyer

—— Coxa 1 male anterodistal corner obtuse P7 basis almost as broad as long ..... *E. pseudaffinis* form A Ledoyer

12 Gnathopod 2 male dactylus two-thirds length of propodus, fitting, when in closed position, into pit on posterior margin of propodus ..... (Figs. 7, 8) *E. puteus*

—— Gnathopod 2 male dactylus less than half length of propodus, lacking pit for reception of tip ..... *Elasmopus* sp. Ledoyer (1978)

Biogeographic remarks

The genus *Elasmopus* is one of the most diverse amphipod genera on the shallow reefs of Mauritius. Thirteen species are now recorded from the island of which at least five species are currently thought to be endemic to Mauritius (or perhaps to the Mascarenes). Three species recorded by Ledoyer (*E. pseudaffinis* form A, *E. pseudaffinis* form B and *Elasmopus* sp.) may also prove to be endemics. Both age and isolation favour the development of endemics (Myers & Giller, 1988). The relatively high endemicity of Mauritius, not only for amphipods, but also for its terrestrial fauna, suggests a long evolutionary history. According to McDougall & Chamalaun (1969) volcanic rocks of Mauritius date only to the early Pliocene (7.8 my) but either Mauritius, a Mauritius progenitor, or other Masacarene islands must, in our opinion, be considerably older, facilitating anagenesis and phylogenesis probably since the late Cretaceous, as in the case of the Seychelles.

Of the Mauritius *Elasmopus* spp., two species are currently thought to be cosmopolitan (*E. spinidactylus* and *E. pectenicrus*), and one species (*E. menurte*), previously known only from the Eastern Indian ocean, is now reported from the Western Indian Ocean.

Of the new species described herein, *E. palu* resembles *E. lapu* from Fiji; *E. steelei* also resembles *E. lapu* as well as *E. ecuadorensis* from the eastern Pacific; *E. pseudinteger* appears to be closely related to *E. integer* from the Society Islands; and *E. puteus* resembles *E. gracilis* a widespread Indo-Pacific species.

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Stegocephalidae (Crustacea: Amphipoda) from Australia and New Zealand, With Descriptions of Eight New Species

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ABSTRACT. The species belonging to the marine amphipod (Crustacea) family Stegocephalidae Dana, 1852 from Australia and New Zealand are reviewed; 25 species are recognized, and a key to the species is presented. Eight new species from the area are described: *Andaniexis andaniexis* n.sp., *Andaniexis elinae* n.sp., *Glorandaniotes sandroi* n.sp., *Glorandaniotes traudlae* n.sp., *Stegocephaloides gunnae* n.sp., *Stegocephaloides ingstadi* n.sp., *Stegocephaloides tori* n.sp., and *Stegocephaloides tucki* n.sp.

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Until recently, only six stegocephalid species, belonging to five genera, were known from Australia and New Zealand: *Andaniotes corpulentus* Stebbing, 1897, *Andaniotes wallaroo* J.L. Barnard, 1972, *Parandania boecki* Stebbing, 1897, *Stegocephalopsis latus* (Haswell, 1879), *Stegosoladidus simplex* (K.H. Barnard, 1930), and *Tetradeion crassum* (Chilton, 1883). Berge (2001a,b) and Berge & Vader (2000) then described six new species and also reported three species as new for the area (in one case re-established *Andaniotes abyssorum* (Stebbing, 1888) as a valid species, see Berge, 2001b). At present, including the species that are recognized herein, the number of stegocephalid species in the area has increased to 25, belonging to 10 different genera.

This paper is a review of the stegocephalid genera and species found in Australia and New Zealand. Phylogenetic relationships between and within the genera are at present not resolved. Pending a revision and a phylogenetic analysis of the entire family (Berge & Vader, 2001b), these relationships will not be discussed herein. Thus, the generic position of all new species described herein strictly follow the diagnoses of genera presented by J.L. Barnard & Karaman (1991).

During the last years, the number of recorded stegocephalid genera and species in Australia and New Zealand has increased significantly. In the present paper, the number of genera found in the area is increased from 5 to 10: *Andaniella* Sars, 1891, *Andaniexis* Stebbing, 1906, *Glorandaniotes* Ledoyer, 1986, *Phippsia* Stebbing, 1906, and *Stegocephaloides* Sars, 1891 are all recorded for the first time in the area. Of these five genera, *Andaniexis, Phippsia* and *Stegocephaloides* have been considered to be mainly North Atlantic and Arctic genera that had not previously been recorded outside the Atlantic. The two other genera, *Andaniella* and *Glorandaniotes*, had both previously been recorded from adjacent areas.

Material and methods

This study is based upon material from the Australian Museum, Sydney (AM) and Museum Victoria, Melbourne (MV).

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All dissected appendages were mounted in polyvinyl-lactophenol, stained with rose-bengal. These appendages were drawn using a Leica compound microscope equipped with a drawing-tube, while the habitus-drawings were made using a Leica dissecting microscope. Mature and immature females were distinguished from males by the presence of oostegites. The classification of setae and setae-groups follows that of Berge (2001a). All scales attached to the figures are 0.1 mm unless otherwise stated.

For each of the new species a diagnosis is included prior to the descriptions (characters used in the diagnoses are omitted in the descriptions). Due to the current uncertain taxonomic status at the generic level (see above) in this family, these diagnoses will separate the present species from all other known stegocephalid taxa. For a discussion on the taxonomic status at the generic level, see Berge & Vader (2001b).

Symbols. A1–2, antenna 1–2; EP3, epimeral plate 3; IP, inner plate; L, labium; LBR, labrum; LMND, left mandible; MX1, maxilla 1; MX2, maxilla 2; MXP, maxilliped; OP, outer plate; P1–7, pereopods 1–7; PLP, palp; RMND, right mandible; ST, setal teeth on the first maxilla; T, telson; U1–3, uropods 1–3.

Key to the stegocephalid species of Australia and New Zealand

Stegocephalopsis latus (Haswell, 1879) is not included due to insufficient descriptions.

1 Basis pereopod 6 more than 1.5 times as broad as basis pereopod 5 2
—— Basis pereopod 6 less than 1.5 times as broad as basis pereopod 5 10

2 Telson as long as peduncle uropod 3 3
—— Telson clearly shorter than peduncle uropod 3 5

3 Telson not longer than broad, distally rounded 4
—— Telson longer than broad, distally pointed and acute ..... *Stegocephaloides tori*

4 Maxilliped palp with 3 articles ..... *Stegosoladidus simplex*
—— Maxilliped palp with 4 articles ..... *Stegosoladidus complex*

5 Coxa 1 about as deep as basis pereopod 1, telson cleft 6
—— Coxa 1 shorter than basis pereopod 1, telson entire 8

6 Pereopod 2 ischium elongate, at least twice as long as broad ..... (see key to the species) *Andaniotes*
—— Pereopod 2 ischium not elongate, about as long as broad 7

7 Antenna 2 peduncle article 4 shorter than 5 ..... *Glorandaniotes traudlae* n.sp.
—— Antenna 2 peduncle article 4 as long as 5 ..... *Glorandaniotes sandroi* n.sp.

8 Antenna 2 conspicuously longer than antenna 1 ..... *Parandania boecki*
—— Antennae equal to subequal 9

9 Telson distally rounded ..... *Andaniexis andaniexis* n.sp.
—— Telson distally pointed ..... *Andaniexis elinae* n.sp.

10 Epistome produced laterally, maxilla 2 not gaping and geniculate 11
—— Epistome unproduced laterally (convex), maxilla 2 gaping and geniculate 13

11 Telson cleft 12
—— Telson entire ..... *Andaniella integripes*

12 Maxilliped palp with 3 articles, almost without setae ..... *Stegosoladidus simplex*
—— Maxilliped palp with 4 articles, heavily setose ..... (see separate key to the species) *Andaniotes*

13 Pereopod 7 with all articles present 15
—— Pereopod 7 with less than 7 articles 14

14 Pereopod 7 with five articles (including coxa) ..... *Tetradeion quatro*
—— Pereopod 7 with three articles (including coxa) ..... *Tetradeion crassum*

15 Telson entire 16
—— Telson cleft 17

16 Epistomal plate large, labrum about as long as broad ..... *Phippsia dampieri*
—— Epistomal plate weakly developed, Labrum longer than broad and triangular ..... *Phippsia angustipalpa*

17 Uropod 3 outer ramus 2-articulate ..... *Stegocephaloides ingstadi* n.sp.
—— Uropod 3 outer ramus 1-articulate 18

18 Epimeral plate 3 posteroventral corner without serrations 19
—— Epimeral plate 3 posteroventral corner with serrations ..... *Phippsia vanhoeffeni*

19 Maxilliped palp dactylus slender and pointed (ordinary) 20
—— Maxilliped palp dactylus distally bifid, setose ..... *Stegocephaloides tucki* n.sp.

20 Accessory flagellum antenna 1 longer (weakly) than flagellum article 1, basis pereopod 4 distally without plumose setae ..... *Stegocephaloides gunnae* n.sp.
—— Accessory flagellum antenna 1 shorter than flagellum article 1, basis pereopod 4 distal anterior and posterior margins with plumose setae ..... *Stegocephaloides tori* n.sp.

Andaniella Sars

Andaniella Sars, 1891: 210.

Type species. *Andania pectinata* Sars, 1883.

Included species. *Andaniella integripes* Bellan-Santini & Ledoyer, 1986; *A. pectinata* (Sars, 1883).

Species found in the area. *Andaniella ?integripes* Bellan-Santini & Ledoyer, 1986.

Material examined. MV J45325, 1 specimen (immature), 40°43.85'S 148°37.46'E, 69.5 m, Tasmania, Eastern Bass Strait.

Remarks. This is the first record of *Andaniella* in the area. The identification is, however, based upon a single immature specimen. Furthermore, considering that the specimen at hand is partly damaged, and that its type locality is the Prince Edward Islands, this identification should be considered as uncertain. It may turn out to belong to a different species, but a final answer must await study of additional material.

Andaniexis Stebbing

Andania Boeck, 1871: 128 (homonym, Lepidoptera).

Andaniexis Stebbing, 1906: 94 (new name).

Type species. *Andania abyssi* Boeck, 1871, selected by Boeck, 1876.

Included species. *Andaniexis abyssi* (Boeck, 1871); *A. americana* Berge *et al.*, 2001; *A. andaniexis* n.sp.; *A. eilae* Berge & Vader, 1997; *A. elinae* n.sp.; *A. gloriosa* Berge *et al.*, 2001; *A. gracilis* Berge & Vader, 1997; *A. lupus* Berge & Vader, 1997; *A. mimonectes* Ruffo, 1975; *A. oculata* Birstein & Vinogradov, 1970; *A. ollii* Berge *et al.*, 2000; *A. spinescens* (Alcock, 1894); *A. spongicola* Pirlot, 1933; *A. stylifer* Birstein & Vinogradov, 1960; *A. subabyssi* Birstein & Vinogradov, 1955; *A. tridentata* Ledoyer, 1986.

Species found in the area. *Andaniexis andaniexis* n.sp. and *A. elinae* n.sp.

Remarks. These are the first records of *Andaniexis* in the area, although the genus has previously been recorded east of Papua New Guinea (*A. stylifer*).

As is evident from Table 1, two of the species within the genus (*A. eilae* and *A. spongicola*) possess a cleft telson, and do thus seem to be more closely related to the genus *Glorandaniotes*. Furthermore, the two species *A. spinescens* and *A. tridentata* have a dorsal carina on pleonites 1–3, and thus seem to be related to the genus *Parandaniexis*. However, pending a revision of the entire family (Berge & Vader, 2001b), no changes are here made in the classification of these species.

Table 1. Differences between species in the genus *Andaniexis*. A dash indicates either that morphological information is missing or that the character is inapplicable.

Description of the characters: **character 1**: pleonites dorsally, a—smooth, b—dentate; **character 2**: antenna 1 flagellum, number of articles; **character 3**: maxilla 1 palp, a—between 4 and 8 robust setae, b—>10 robust setae; **character 4**: maxilliped inner plate number of nodular setae; **character 5**: coxa 4 distally, a—broad, b—narrow/pointed; **character 6**: pereopod 4 basis, a—with long setae, b—without long setae; **character 7**: pereopod 7 basis anteriorly, a—straight, b—weakly concave; **character 8**: telson apically, a—rounded, b—pointed; **character 9**: telson, a—entire, b—cleft.

	characters								
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Andaniexis abyssi	a	5	a	2	a	b	a	b	a
Andaniexis americana	a	5	a	1	b	a	b	a	a
Andaniexis andaniexis	a	5	a	1	a	a	a	a	a
Andaniexis australis	a	5	a	1	a	b	b	b	a
Andaniexis eilae	a	4	a	2	b	a	a	a	b
Andaniexis elinae	a	5	a	1	a	a	a	b	a
Andaniexis gloriosa	a	5	a	1	b	b	a	b	a
Andaniexis gracilis	a	5	a	2	b	b	b	a	a
Andaniexis lupus	a	5	a	2	a	a	a	b	a
Andaniexis mimonectes	a	4	a	3	b	a	a	a	a
Andaniexis oculata	a	5	a	–	a	b	b	b	a
Andaniexis ollii	a	5	a	1	a	b	a	b	a
Andaniexis spinescens	b	–	–	–	b	–	a	a	a
Andaniexis spongicola	a	–	a	2	b	a	a	a	b
Andaniexis stylifer	a	5	b	2	a	a	b	a	a
Andaniexis subabyssi	a	4	a	–	a	a	b	a	a
Andaniexis tridentata	b	5	a	–	b	b	a	a	a

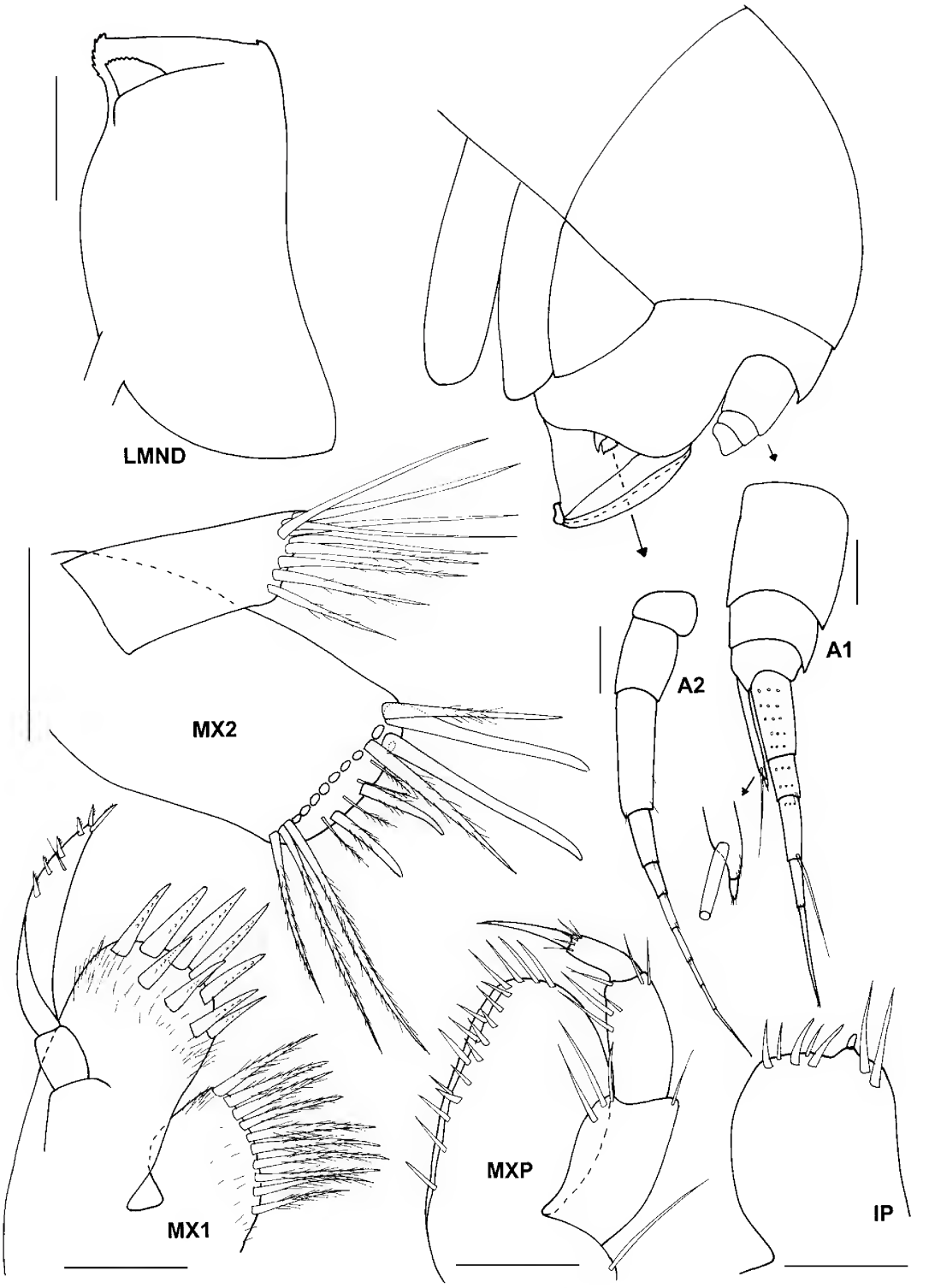

Fig. 1. *Andaniexis andaniexis* n.sp. holotype. IP, inner plate of maxilliped.

***Andaniexis andaniexis* n.sp.**

Figs. 1–3

Type material. HOLOTYPE: AM P52714, ♀ 4 mm, 16°37.81'S 146°23.08'E, 1000 m (QLD-932), east of Flynn Reef, Queensland, Australia, 06 Jun. 1993. Collector: J.K. Lowry & party on RV "Sunbird" (SEAS project trap 3, transect 1). PARATYPE: AM P52716, ♀ 5 mm, 16°37.81'S 146°23.08'E, 1000 m (QLD-949), east of Flynn Reef, Queensland, Australia, 07 Jun. 1993. Collector: J.K. Lowry & party on RV "Sunbird" (SEAS project trap 2, transect 2).

Distribution. Known only from the type locality.

Diagnosis (see also Table 1): Pleonites dorsally smooth. Antenna 1 flagellum with 5 articles, accessory flagellum longer than flagellum article 1. Antenna 2 peduncle article 4 shorter than article 5. Epistome produced laterally, epistomal plate present. Labrum shorter than broad, both lobes reduced. Mandibular incisor smooth, transverse. Lacinia mobilis reduced, not expanded laterally. Maxilla

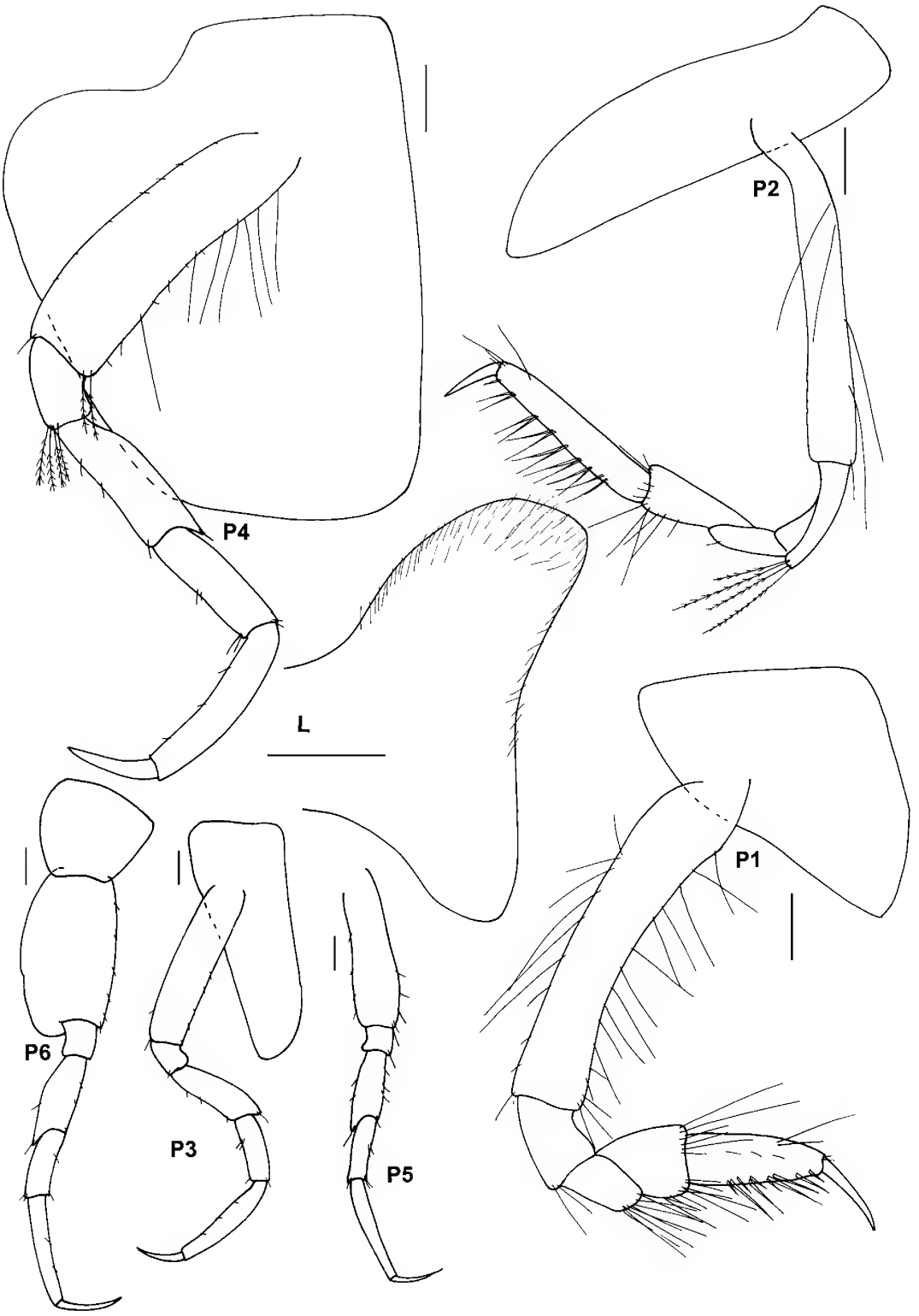

Fig. 2. *Andaniexis andaniexis* n.sp. holotype.

1 outer plate with ST in two parallel rows, palp 2-articulate. Maxilla 2 outer plate not gaping and geniculate. Maxilliped inner plate with one nodular seta. Coxa 4 distally broad. Pereopod 6 basis expanded. Articulation present between urosomites 2 and 3. Uropod 3 outer ramus 2-articulate. Telson about as long as broad, apically rounded, entire.

Description. Rostrum reduced, inconspicuous. Antenna 1 weakly longer than antenna 2; accessory flagellum article 2 present. Antenna 2 peduncle articles 3–5 shorter than flagellum; article 3 short, about as long as broad. Epistome rectangular, with a long ridge on each side; epistomal plate produced into a small elongate medial ridge covering the entire epistome. Maxilla 1 palp reaching above the apex of outer plate; outer plate distally rounded; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A–C present, part of second row; inner plate with pappose setae. Maxilla 2 ordinary; outer plate

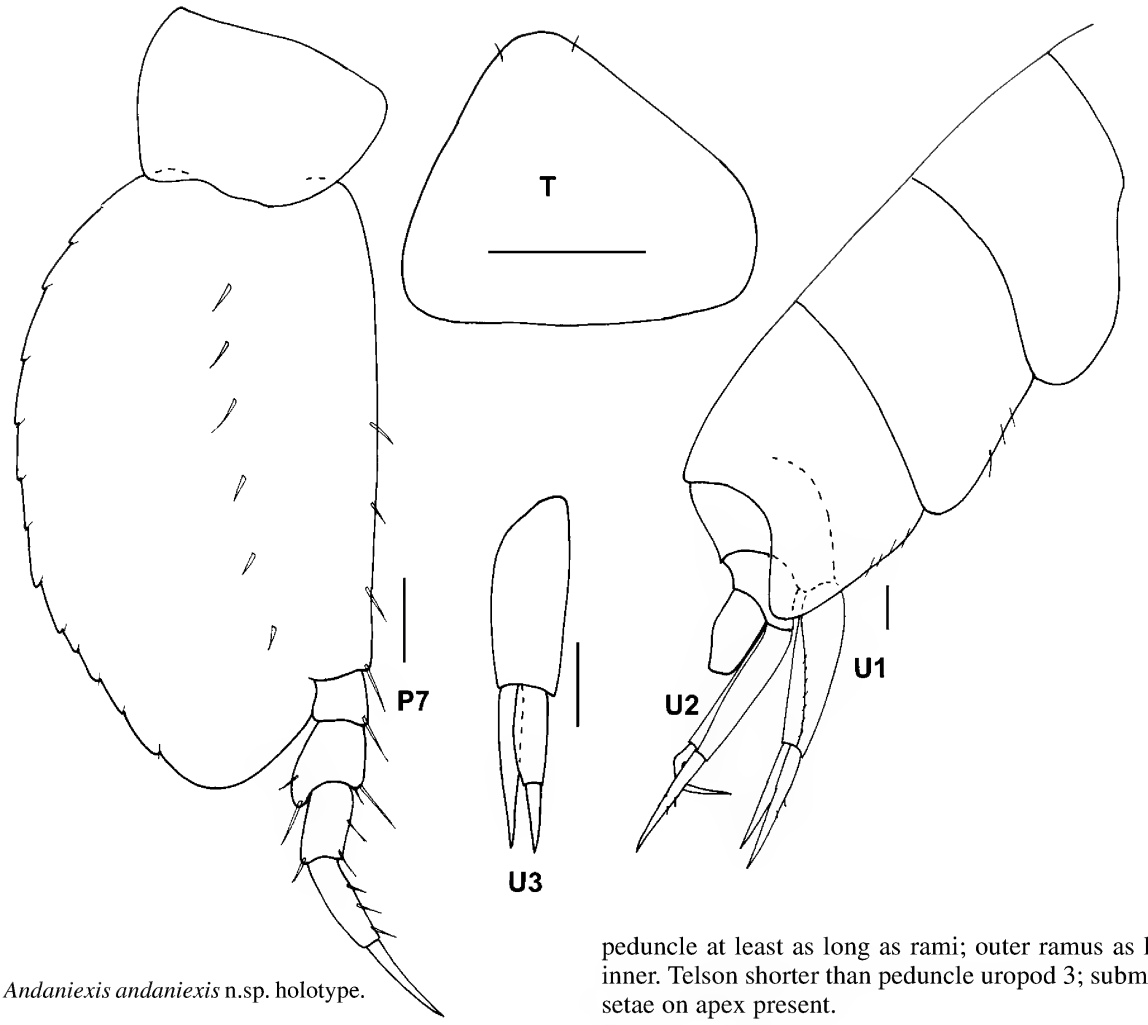

Fig. 3. *Andaniexis andaniexis* n.sp. holotype.

setae distally simple; inner plate setae row A covering the entire margin, clearly separated from row B; row A setae pappose; row B setae proximally pappose, distally without cusps; row C present; row D present, reduced, 1–3 long slender setae distally. Maxilliped palp 4-articulate; article 2 distally unproduced; dactylus distally simple, pointed; inner plate not exceeding base of palp article 2; medial setae-row transverse with setae simple; distal setae-row present; inner setae-row reduced to one or two setae; outer plate with outer setae-row submarginal, with long robust setae; inner setae-row well developed with long robust setae, appressed to outer setae-row; distal setae-group absent. Labium distally broad, oval. Coxae and bases on the pereopods smooth. Coxae 1–3 contiguous. Pereopod 1 coxa not as deep as basis; propodus subrectangular. Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length to breadth exceeding 1.5, distal posterior margin with plumose setae; propodus subrectangular, palm absent. Pereopod 4 basis anterior margin with long setae, posterior margin without long setae; plumose setae on anterior distal margin; ischium with plumose setae on posterior distal margin. Pereopod 6 basis about twice as broad as basis on pereopod 5. Pereopod 7 basis anterior margin straight; distally rounded; medial row of setae present; setae short and robust. Oostegites on pereopods 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle longer than rami; outer ramus as long as inner. Uropod 3 peduncle at least as long as rami; outer ramus as long as inner. Telson shorter than peduncle uropod 3; submarginal setae on apex present.

Male. Unknown.

Etymology. Based upon the general morphology of the present species, it is a typical member of the genus, hence the name.

Remarks. For differences among the world's species of *Andaniexis*, see Table 1.

Andaniexis elinae n.sp.

Figs. 4, 5

Type material. HOLOTYPE: MV J40614, ♀ 5 mm, 42°2.20'S 148°38.70'E, 800 m, off Freycinet Peninsula, Tasmania, Australia, 27 Jul. 1986. Collector: M.F. Gomon and party. PARATYPE: MV J24061, immature 3 mm, 42°2.20'S 148°38.70'E, 800 m, off Freycinet Peninsula, Tasmania, Australia, 27 Jul. 1986. Collector: M.F. Gomon and party.

Additional material. MV J24051, 4 specimens, 34°57.90'S 150°20.20'E, 503 m, New South Wales, off Nowra, 14 Jul. 1986; MV J24055, 4 specimens, 38°25.00'S 149°0.00'E, 1500 m, Victoria, south of Point Hicks, 22 Jul. 1986; MV J24058, 7 specimens, 38°19.60'S 149°24.30'E, 930 m, Victoria, south of Point Hicks, 23 Jul. 1986; MV J24064, 5 specimens, 41°57.50'S 148°37.90'E, 400 m, Tasmania, off Freycinet Peninsula, 27 Jul. 1986; MV J40617, 1 specimen, 38°25.90'S 148°58.60'E, 1850 m, Victoria, south of Point Hicks, 22 Jul. 1986; MV J40619, 20 specimens, 38°21.90'S 149°20.00'E, 1000 m, Victoria, south of Point Hicks, 23 Jul. 1986; MV J40622, 2 specimens, 38°16.40'S 149°27.60'E, 800 m, Victoria, south of Point Hicks, 23 Jun. 1986.

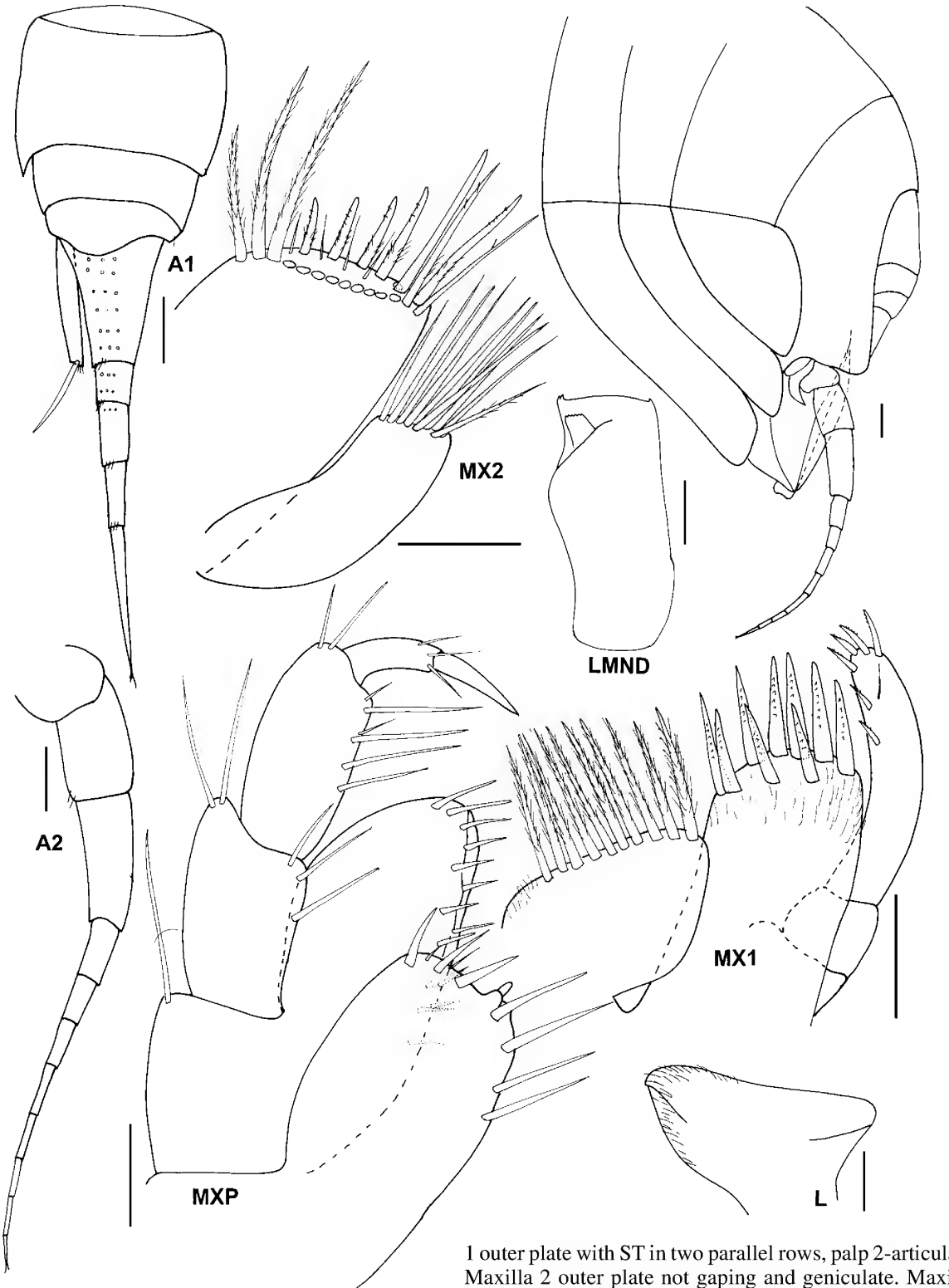

Fig. 4. *Andaniexis elinae* n.sp. holotype.

Distribution. New South Wales, Victoria and Tasmania, 400–1850 m.

Diagnosis (see also Table 1). Pleonites dorsally smooth. Antenna 1 flagellum with 5 articles, accessory flagellum not longer than flagellum article 1. Antenna 2 peduncle article 4 shorter than article 5. Epistome produced laterally, epistomal plate present. Labrum shorter than broad, both lobes reduced. Mandibular incisor smooth, transverse. Lacinia mobilis reduced, not expanded laterally. Maxilla 1 outer plate with ST in two parallel rows, palp 2-articulate. Maxilla 2 outer plate not gaping and geniculate. Maxilliped inner plate with one nodular seta. Coxa 4 distally broad. Pereopod 6 basis expanded. Articulation present between urosomites 2 and 3. Uropod 3 outer ramus 2-articulate. Telson about as long as broad, apically pointed, entire.

Description. Rostrum reduced, inconspicuous. Antenna 1 about as long as antenna 2; accessory flagellum article 2 absent. Antenna 2 peduncle articles 3–5 shorter than flagellum; article 3 short, about as long as broad. Epistome rectangular, with a long ridge on each side; epistomal plate produced into a small elongate medial ridge covering the entire epistome. Maxilla 1 palp reaching above the apex of

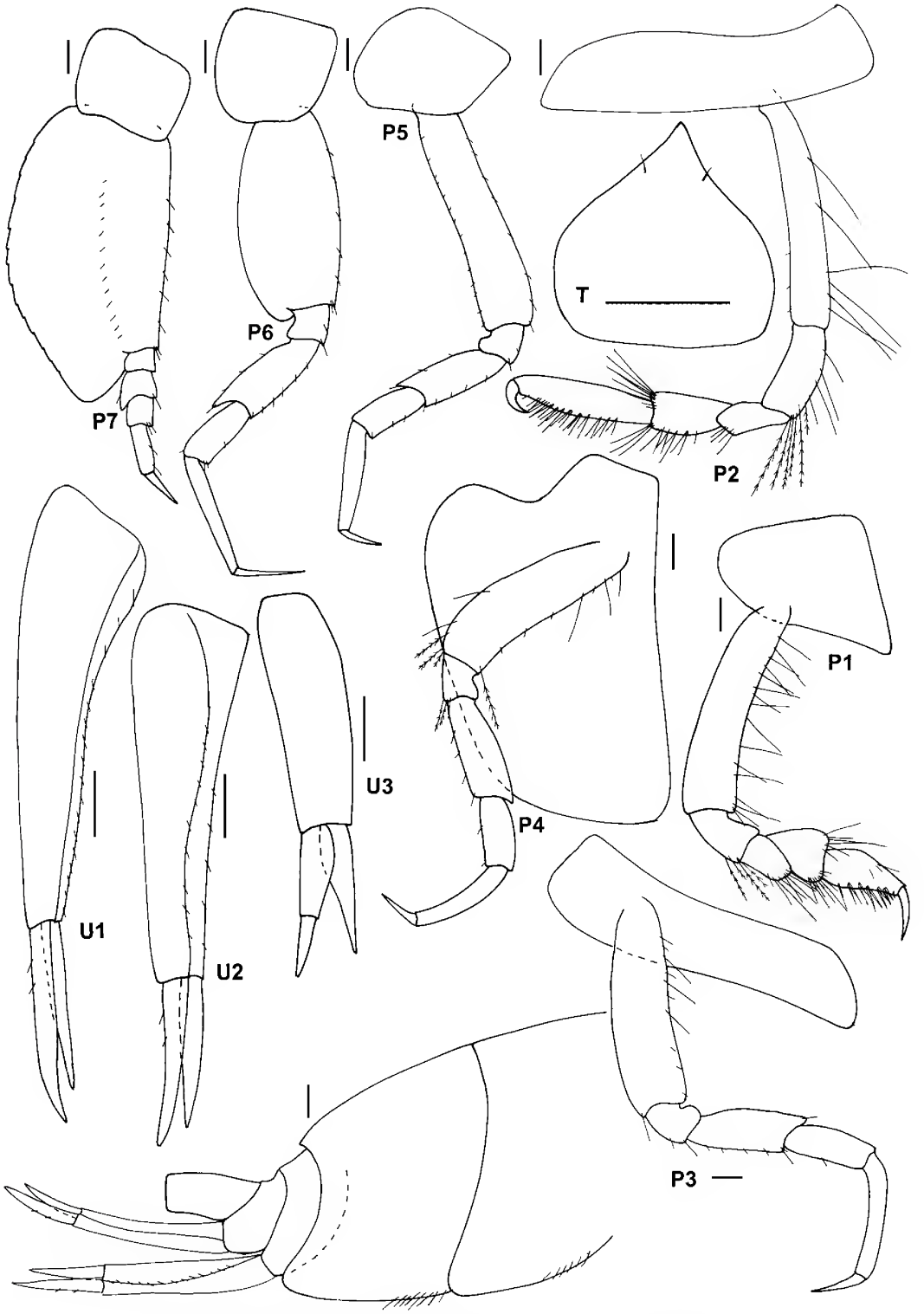

Fig. 5. *Andaniexis elinae* n.sp. holotype, except *U3*—female A MV J40619.

outer plate; outer plate distally rounded; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present, part of second row; ST B present; ST C present; inner plate with pappose setae. Maxilla 2 ordinary; outer plate setae distally simple; inner plate setae row A covering the entire margin; clearly separated from row B; row A setae pappose; row B setae proximally pappose; distally with cusps present; row C present; row D present, reduced, 1–3 long slender setae distally. Maxilliped palp 4-articulate; article 2 distally unproduced; dactylus distally simple, pointed; inner plate not exceeding base of palp article 2; medial setae-row transverse with simple setae; distal setae-row present; inner setae-row not reduced; outer plate with outer setae-row submarginal with long robust setae; inner setae-row well developed with long robust setae, row appressed to outer setae-row; distal setae-group absent. Labium distally broad, oval. Coxae and bases on the pereopods smooth. Coxae 1–3 contiguous. Pereopod 1 coxa not as deep as basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length

to breadth exceeding 1.5, distal posterior margin with plumose setae; propodus subrectangular, palm absent. Pereopod 4 basis anterior and posterior margins with long setae, with plumose setae on distal anterior and posterior margins; ischium with plumose setae on posterior distal margin. Pereopod 6 basis about twice as broad as basis on pereopod 5. Pereopod 7 basis anterior margin straight, distally rounded; medial row of setae present, setae short and robust. Oostegites on pereopod 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle longer than rami; outer ramus longer than inner. Uropod 3 peduncle at least as long as rami; outer ramus longer than inner. Telson shorter than peduncle uropod 3; submarginal setae on apex present.

Male. Unknown.

Etymology. Named after the first author's sister Astrid Eline Berge.

Remarks. For differences between the world's species of *Andaniexis*, see Table 1.

Andaniotes Stebbing

Andaniotes Stebbing, 1897: 30.
Andaniotes.–Berge, 2001b (revision).

Type species. *Anonyx corpulentus* Thomson, 1882.

Included species. *Andaniotes abyssorum* (Stebbing, 1888); *A. bagabag* Lowry & Stoddart, 1995; *A. corpulentus* (Thomson, 1882); *A. karkar* Lowry & Stoddart, 1995; *A. linearis* K.H. Barnard, 1930; *A. lowryi* Berge, 2001b; *A. pooh* Berge, 2001b; *A. poorei* Berge, 2001b; *A. pseudolinearis* Berge, 2001b; *A. wallaroo* J.L. Barnard, 1972; *A. wollongong* Berge, 2001b.

Species found in the area. *Andaniotes abyssorum* (Stebbing, 1888); *A. corpulentus* (Thomson, 1882); *A. lowryi* Berge, 2001b; *A. pooh* Berge, 2001b; *A. poorei* Berge, 2001b; *A. wallaroo* J.L. Barnard, 1972; *A. wollongong* Berge, 2001b.

Remarks. For a revision of *Andaniotes*, and details about the species, see Berge, 2001b.

Key to the world species of *Andaniotes*

See also Table 2 for male specimens.

1 Pereopod 6 basis medially with a long row (covering the entire length of basis) of robust slender setae ..... *A. linearis*
—— Pereopod 6 basis medially without setae or with a short distal row of long plumose setae 2

2 Pereopod 6 basis not more than 1.5 times as broad as basis pereopod 5, posterior margin faintly concave 3
—— Pereopod 6 basis about twice as broad as basis pereopod 5, posterior margin linear or convex 4

3 Maxilliped inner plate with 4 nodular setae, males with outer ramus enlarged (stout, strongly curved upwards) on both uropod 1 and 2 ..... *A. pooh*
—— Maxilliped inner plate with 3 nodular setae, males with outer ramus enlarged (stout, strongly curved upwards) on uropod 2 only ..... *A. poorei*

4 Pereopod 7 merus conspicuously enlarged, posterior lobe about twice as long as carpus ..... *A. wallaroo*
—— Pereopod 7 merus not conspicuously enlarged 5

5 Pereopod 7 basis similar to basis on pereopod 6, posterior margin straight or slightly convex 6
—— Pereopod 7 basis broader and longer than basis on pereopod 6, basis conspicuously subovate 8

6 Oostegites on pereopods 3–5 7
—— Oostegites on pereopods 4–5 ..... *A. karkar*

7 Pereopod 4 basis distally with plumose setae on both posterior and anterior margin ..... *A. lowryi*
—— Pereopod 4 basis distally with plumose setae only on the anterior margin ..... *A. bagabag*

8 Antenna 1 flagellum article 1 at least 1.5 times longer than articles 2–4 combined ..... *A. pseudolinearis*
—— Antenna 1 flagellum article 1 about as long as articles 2–4 combined 9

9 Gills on pereopods 2 and 3 long and narrow (shape similar to that of the oostegites), distinct from those on pereopods 4 and 5 ..... *A. wollongong*

—— Gills on pereopods 2 and 3 similar to those on pereopods 4 and 5 10

10 Epistome anteriorly broad and rounded ..... *A. abyssorum*

—— Epistome anteriorly subrectangular ..... *A. corpulentus*

Table 2. Comparison of male characteristics of the genus *Andaniotes* (for three of the species, a male specimen has not been reported). Character states (reduced, ordinary and enlarged) are based upon a comparison with the females of the respective species.

species, males	urosome	uropod 1 outer ramus	uropod 2 outer ramus	uropod 3 rami
Andaniotes abyssorum	enlarged	enlarged	enlarged	reduced
Andaniotes bagabag	males unknown			
Andaniotes corpulentus	enlarged	enlarged	ordinary	reduced
Andaniotes karkar	enlarged	enlarged	ordinary	reduced
Andaniotes linearis	males unknown			
Andaniotes lowryi	enlarged	enlarged	ordinary	reduced
Andaniotes pooh	enlarged	enlarged	enlarged	ordinary
Andaniotes poorei	enlarged	ordinary	enlarged	ordinary
Andaniotes pseudolinearis	enlarged	ordinary	enlarged	ordinary
Andaniotes wallaroo	enlarged	enlarged	ordinary	reduced
Andaniotes wollongong	males unknown			

One of the main characteristics of this genus is the conspicuous sexual dimorphism found mainly on the urosome, but also to a varying degree on the epistome and pereopods 1 and 2. Males of all *Andaniotes* species, (a male has not yet been recorded for three species, see Table 2), possess an enlarged urosome. Furthermore, the outer ramus on uropod 1 and/or 2 may be enlarged, and the rami of uropod 3 may be reduced. To help identification of also male specimens, this sexual dimorphism on the urosome is summarized in Table 2. Except for *A. linearis* and *A. pseudolinearis*, the present genus is endemic to the area, and is, by far, represented with the highest number of species (7).

Glorandaniotes Ledoyer

Glorandaniotes Ledoyer, 1986: 957.

Type species. *Glorandaniotes fissicaudata* Ledoyer, 1986.

Included species. *Glorandaniotes fissicaudata* Ledoyer, 1986; *G. sandroi* n.sp.; *G. traudlae* n.sp.

Species found in the area. *Glorandaniotes sandroi* n.sp. and *G. traudlae* n.sp.

Remarks. These are the first records of *Glorandaniotes* from the area.

Glorandaniotes sandroi n.sp.

Figs. 6, 7

Type material. HOLOTYPE: MV J40630, ♀ 5 mm: 38°52.6'S 148°25.2'E, 130 m (fine sand), 100 km NE of North Point, Flinders Island, Eastern Bass Strait, Tasmania, Australia, 15 Nov. 1981. Collector: R. Wilson. PARATYPES: MV J40629, 1♂ and 6♀♀: 38°52.6'S 148°25.2'E, 130 m (fine sand), 100 km NE of North Point, Flinders Island, Eastern Bass Strait, Tasmania, Australia, 15 Nov. 1981. Collector: R. Wilson.

Distribution. Known only from the type locality.

Diagnosis. Pleonites dorsally smooth. Antenna 1 flagellum with 4 articles. Antenna 2 peduncle article 4 slightly longer than article 5. Epistome produced laterally, epistomal plate present. Labrum shorter than broad, both lobes reduced. Mandibular incisor smooth, transverse. Lacinia mobilis reduced, not expanded laterally. Maxilla 1 outer plate with ST in two parallel rows, palp uni-articulate. Maxilla 2 outer plate not gaping and geniculate. Coxa 4 distally broad. Pereopod 6 basis expanded. Uropod 3 outer ramus 2-articulate. Articulation between urosomites 2 and 3 present. Telson about as long as broad, rounded, cleft.

Description. Rostrum reduced, inconspicuous. Antenna 1 shorter than antenna 2; accessory flagellum article 2 present. Antenna 2 peduncle articles 3–5 longer than flagellum; article 3 short, about as long as broad. Epistome rectangular, with a long ridge on each side; epistomal plate produced into a small elongate medial ridge covering the entire epistome (similar to *G. traudlae*, see Fig. 8). Maxilla 1 palp reaching above the apex of outer plate; outer plate distally rounded; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A–C present, part of second row; inner plate with pappose setae. Maxilla 2 ordinary; outer plate setae distally simple; inner plate setae row A covering the entire margin, clearly separated from row B; row A setae pappose; row B setae proximally pappose; distally with cusps present; row C present; row D absent. Maxilliped palp 4-articulate; article 2 distally unproduced; dactylus distally simple, pointed; inner plate not exceeding base of palp article 2; 2 nodular setae; medial setae-row transverse with pectinate setae; distal setae-row present; inner setae-row not reduced; outer plate with outer setae-row marginal with long robust setae; inner setae-row reduced, setae short and simple, parallel but not appressed to outer setae-row; distal setae-group absent. Labium distally broad, oval. Coxae and bases on the pereopods smooth. Coxae 1–3 contiguous. Pereopod 1 coxa deeper than basis; propodus distally narrowing.

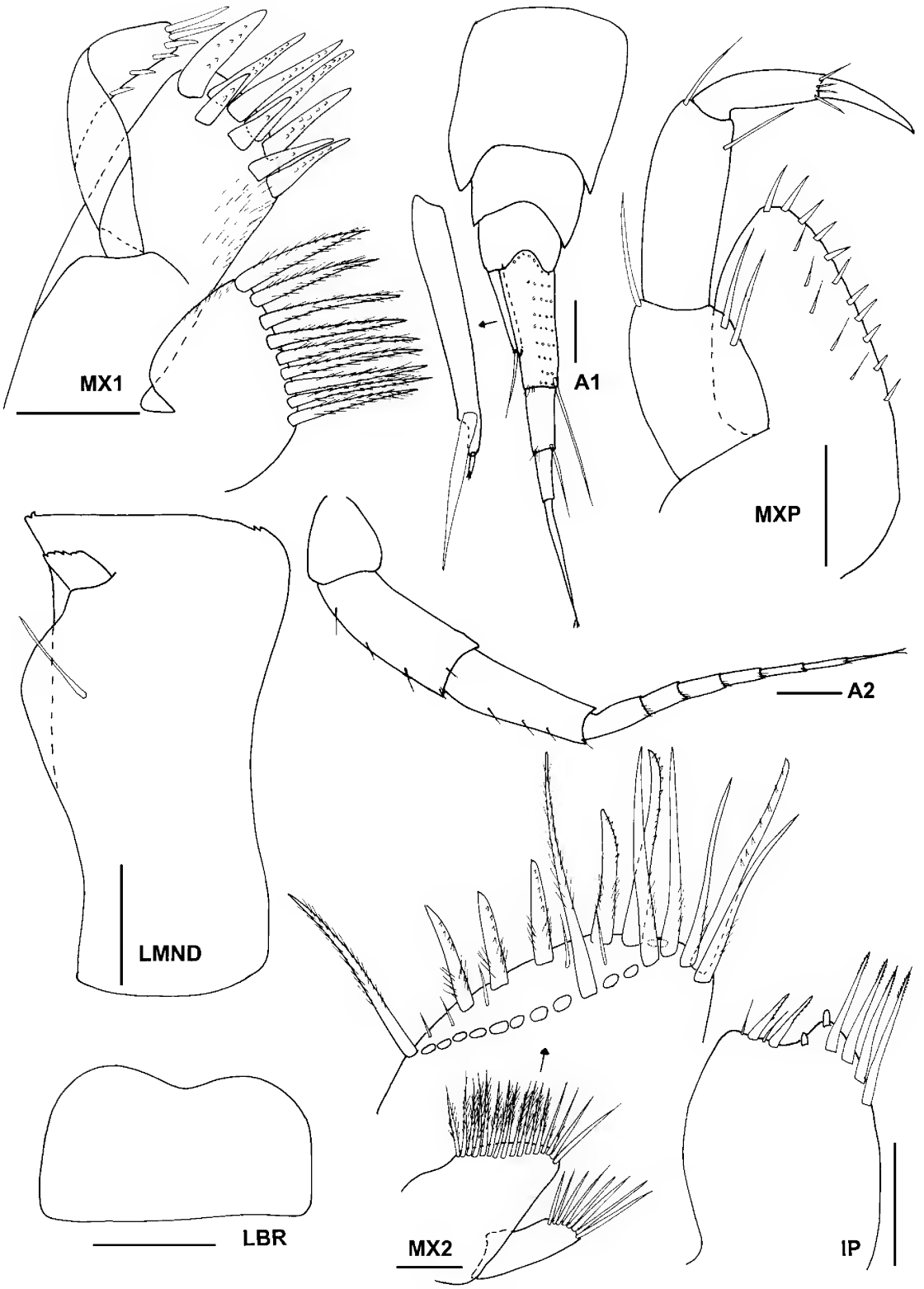

Fig. 6. *Glorandaniotes sandroi* n.sp. holotype. *IP*, inner plate of maxilliped.

Pereopod 2 general appearance like pereopod 1; ischium not elongate, distal posterior margin with plumose setae; propodus subrectangular but distally narrowing, palm absent. Pereopod 4 basis posterior margin with long setae present, plumose setae on distal anterior and posterior margins; ischium with plumose setae on distal posterior margin. Pereopod 6 basis more than twice as broad as basis on pereopod 5, medially with a row of long plumose setae. Pereopod 7 basis anterior margin straight, distally rounded; medial row of setae present, setae short and robust. Oostegites on pereopod 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle longer than rami; outer ramus longer than inner. Uropod 3 peduncle at least as long as rami; outer ramus longer than inner. Telson shorter than peduncle uropod 3; submarginal setae on apex of each lobe present.

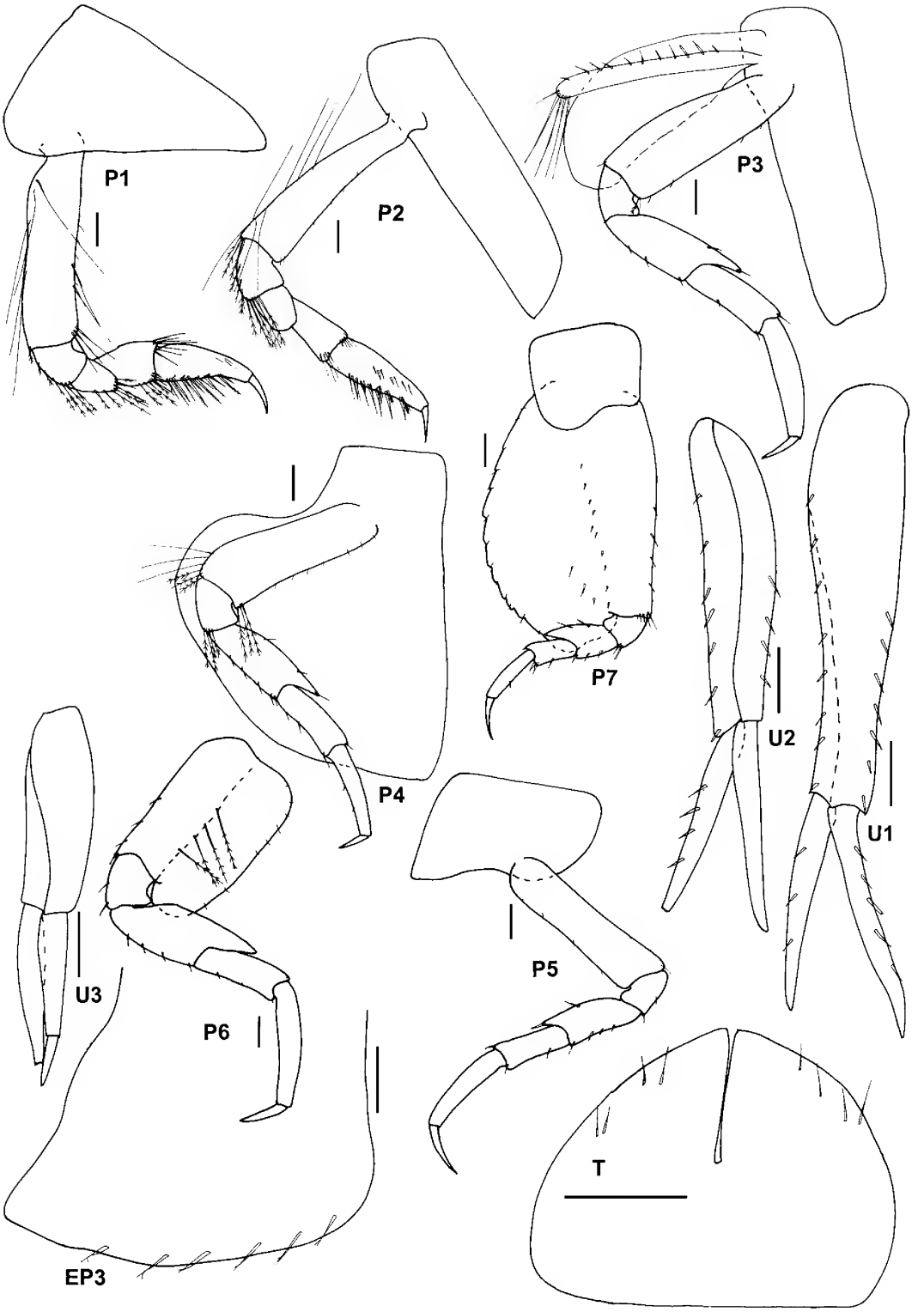

Fig. 7. *Glorandaniotes sandroi* n.sp. holotype.

Male. Pereopod 2 propodus equally sized in males and females, urosome ordinary (similar to females).

Etymology. Named after Prof Sandro Ruffo (Verona), grand old man of amphipod research.

Remarks. The general morphology of *Glorandaniotes sandroi* is very similar to that of *G. traudlae* (habitus only figured for the latter, see below). The two species are separated mainly on the absence of an articulation between urosomites 2 and 3 in *G. traudlae*, the long peduncle article 4 on the second antenna in *G. sandroi*, and the different setation on pereopod 4. Furthermore, the males of *G. sandroi* do not possess an enlarged propodus on pereopod 2, as in *G. traudlae*.

Both new species described herein are separated from the type species by their small and inconspicuous epistomal plate.

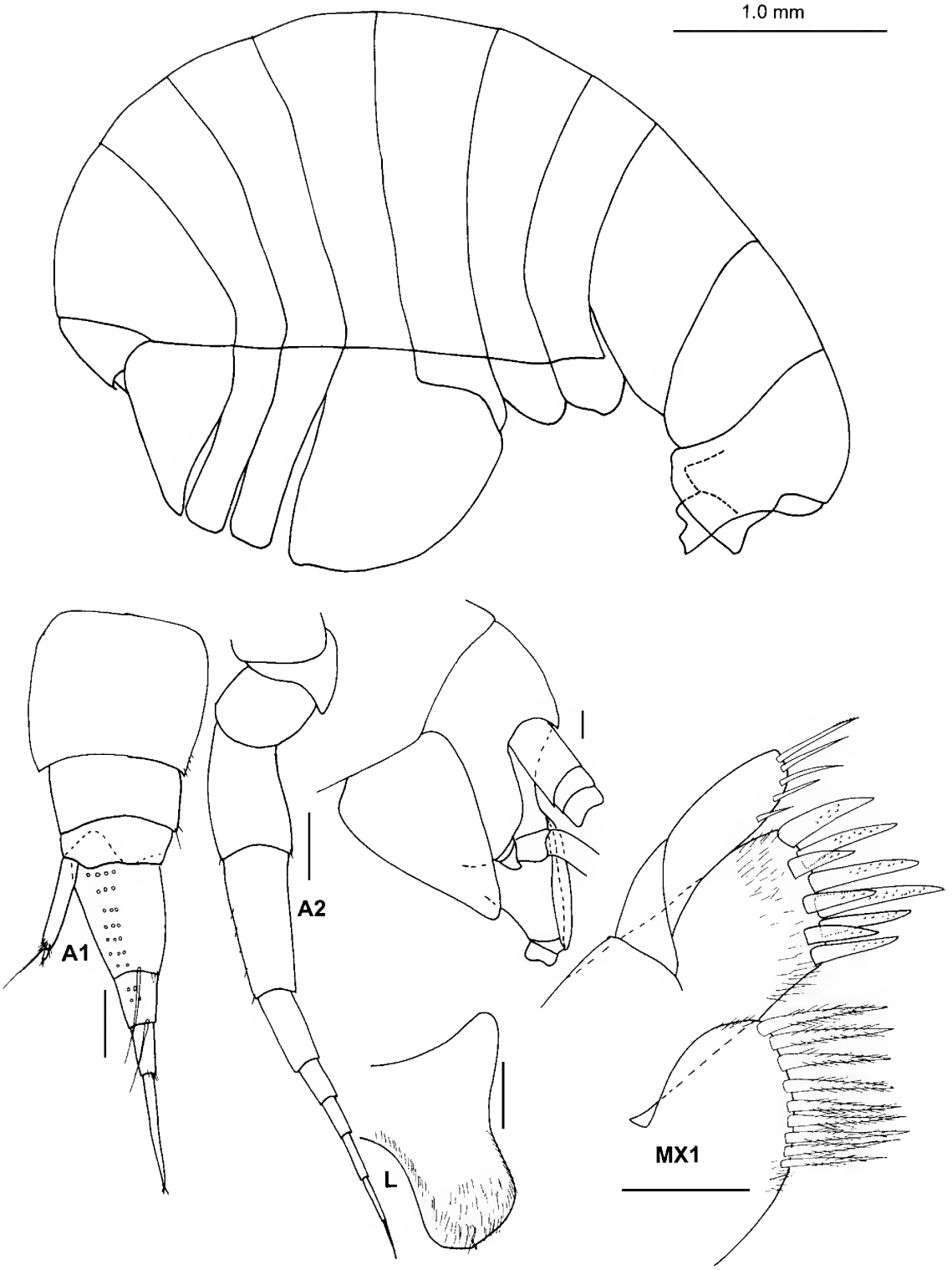

Fig. 8. *Glorandaniotes traudlae* n.sp. holotype, except habitus—paratype female B.

Glorandaniotes traudlae n.sp.

Figs. 8–10

Type material. HOLOTYPE: AM P47042, ♀ 4 mm, 34°32.09'S 151°12.55'E, 200 m (NSW-797), off Wollongong, New South Wales, Australia, 07 May 1993. Collector: P. Freewater & party on MV "Robin E" (SEAS project, trap 1, transect 2). PARATYPES: AM P60468, 122 specimens (♂♂ and ♀♀), 3–5 mm, 34°32.09'S 151°12.55'E, 200 m (NSW-797), off Wollongong, New South Wales, Australia, 07 May 1993. Collector: P. Freewater & party on MV "Robin E" (SEAS project, trap 1, transect 2).

Distribution. Known only from the type locality.

Diagnosis. Pleonites dorsally smooth. Antenna 1 flagellum with 4 articles. Antenna 2 peduncle article 4 shorter than article 5. Epistome produced laterally, epistomal plate present. Labrum shorter than broad, both lobes reduced.

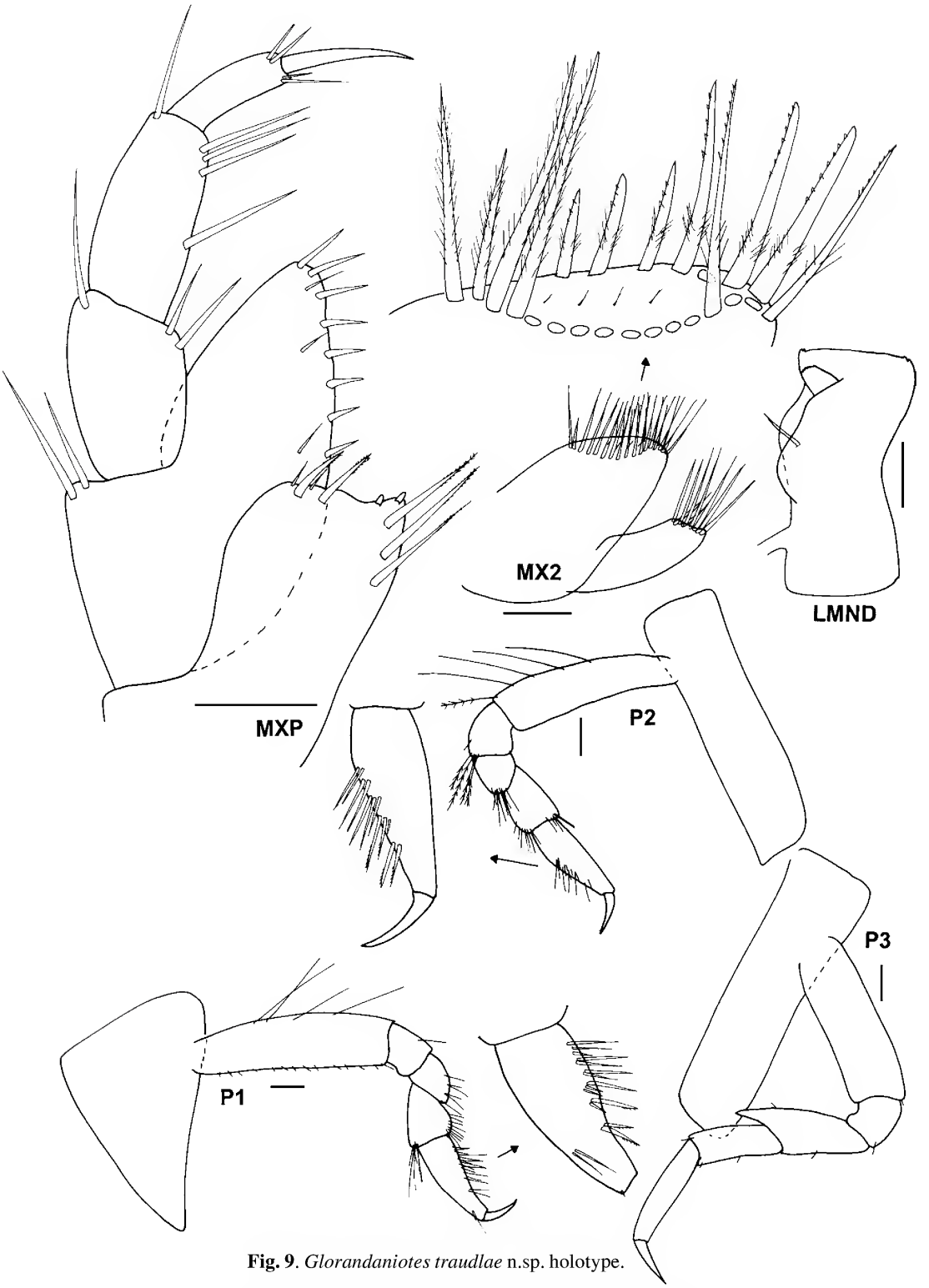

Fig. 9. *Glorandaniotes traudlae* n.sp. holotype.

Mandibular incisor smooth, transverse. Lacinia mobilis reduced, not expanded laterally. Maxilla 1 outer plate with ST in two parallel rows, palp uni-articulate. Maxilla 2 outer plate not gaping and geniculate. Coxa 4 distally broad. Pereopod 6 basis expanded. Uropod 3 outer ramus 2-articulate. Articulation between urosomites 2 and 3 absent. Telson about as long as broad, rounded, cleft.

Description. Rostrum reduced, inconspicuous. Antenna 1 about as long as antenna 2; accessory flagellum article 2 present. Antenna 2 peduncle articles 3–5 longer than flagellum; article 3 short, about as long as broad. Epistome rectangular, with a long ridge on each side; epistomal plate produced into a small elongate medial ridge covering the entire epistome. Maxilla 1 palp reaching above the apex of outer plate; outer plate distally subrectangular; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A–C present, part of second row; inner plate with pappose setae. Maxilla 2 ordinary; outer plate setae distally simple; inner plate setae row A covering the entire margin, clearly separated from row B; row A setae pappopectinate; row B setae proximally pappose, distally

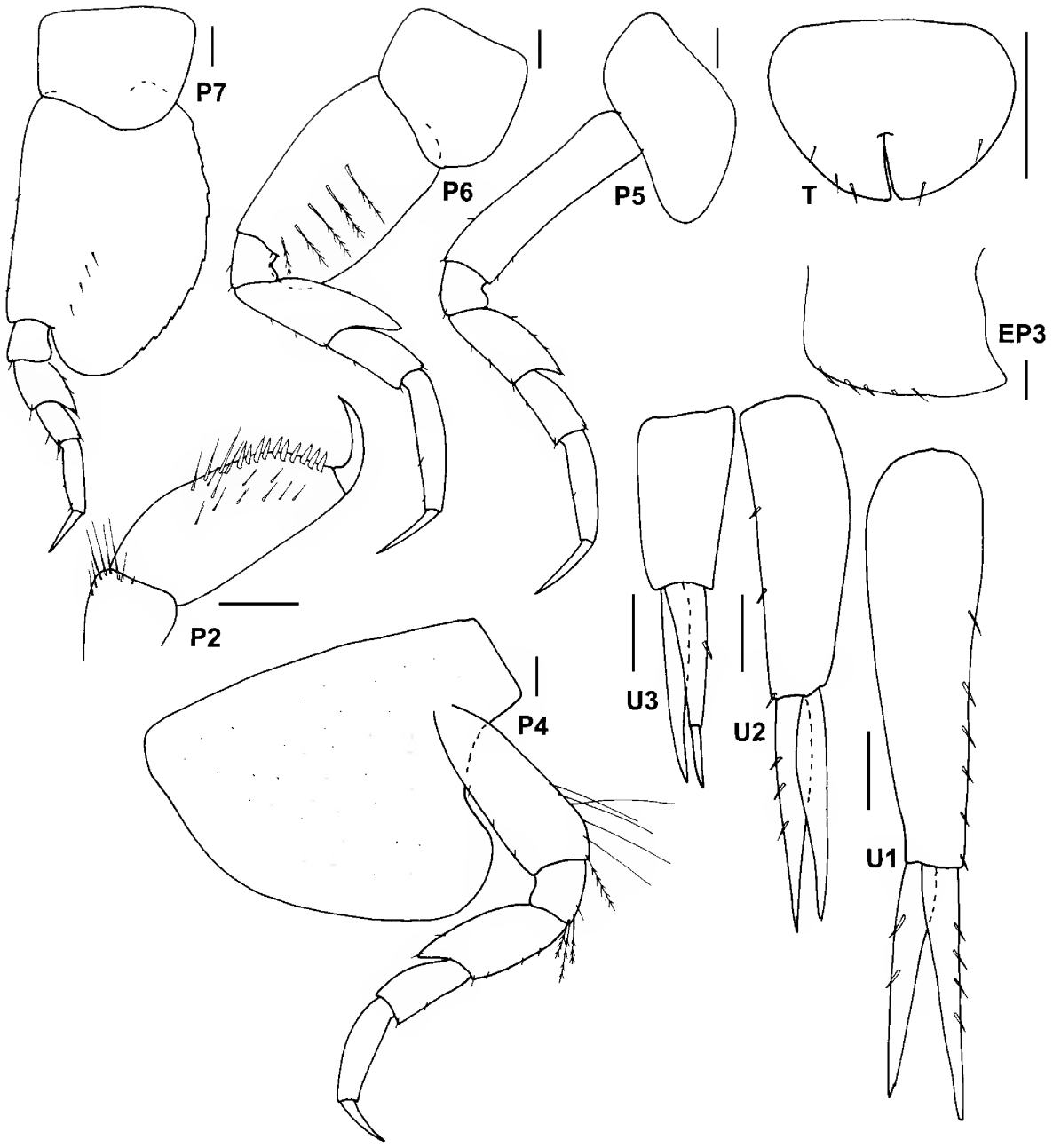

Fig. 10. *Glorandaniotes traudlae* n.sp. holotype, except *P2*—paratype male A and *EP3*—paratype female B.

with cusps present; row C present; row D absent. Maxilliped palp 4-articulate; article 2 distally unproduced; dactylus distally simple, pointed; inner plate not exceeding base of palp article 1; 2 nodular setae; medial setae-row transverse with pectinate setae; distal setae-row present; inner setae-row not; outer plate with outer setae-row marginal, setae long robust; inner setae-row reduced with short and simple setae; row parallel but not appressed to outer setae-row; distal setae-group absent. Labium distally broad, oval. Coxae and bases on the pereopods covered with setae; setae very short. Coxae1–3 contiguous. Pereopod 1 coxa deeper than basis; propodus distally narrowing. Pereopod 2 general appearance like pereopod 1; ischium not elongate, distal posterior margin with plumose setae; propodus distally narrowing, palm absent. Pereopod 4 basis posterior margin with long setae, plumose setae on distal posterior margin; ischium with plumose setae on distal posterior margin. Pereopod 6 basis more than twice as broad as basis on pereopod 5, medially with a row of long plumose setae. Pereopod 7 basis anterior margin straight, distally rounded; medial row ofsetae present, setae short and robust. Oostegites on pereopod 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle longer than rami; outer ramus longer than inner. Uropod 3 peduncle longer than half the length of rami; outer ramus longer than inner. Telson shorter than peduncle uropod 3; submarginal setae on apex of each lobe present.

Male. Pereopod 2 propodus larger in males than in females, urosome ordinary (similar to females).

Etymology. Named after Dr Traudl Krapp (Bonn), great friend and indefatigable amphipod worker.

Remarks. See remarks under *Glorandaniotes sandroi*.

Parandania Stebbing

Parandania Stebbing, 1899: 206.

Type species. *Andania boecki* Stebbing, 1888. Monotypic genus.

Species found in the area. *Parandania boecki* (Stebbing, 1888).

Material examined. AM P50233, 121 specimens, 16°37.81'S 146°23.08'E, 1000 m, east of Flynn Reef, far north Queensland, Australia.

Remarks. Marine cosmopolitan species, 300–2200 m.

Phippsia Stebbing

Aspidopleurus Sars, 1891: 203 (homonym, Pisces).
Phippsia Stebbing, 1906: 89 (new name).
Phippsia.–Berge & Vader, 2000: 150 (revision).

Type species. *Stegocephalus gibbosus* Sars, 1883.

Included species. *Phippsia angustipalpa* Berge & Vader, 2000; *P. dampieri* Berge & Vader, 2000; *P. gibbosa* (Sars, 1883), *P. roemeri* Schellenberg, 1925, *P. unihamata* Berge & Vader, 2000; *P. vanhoeffeni* (Schellenberg, 1926).

Species found in the area. *Phippsia angustipalpa* Berge & Vader, 2000, *P. dampieri* Berge & Vader, 2000 and *P. vanhoeffeni* (Schellenberg, 1926).

Remarks. For a revision of *Phippsia*, and details about the species, see Berge & Vader, 2000.

Stegocephaloides Sars

Stegocephaloides Sars, 1891: 201.

Type species. *Stegocephalus christianiensis* Boeck, 1871.

Included species. *Stegocephaloides attingens* K.H. Barnard, 1916; *S. auratus* (Sars, 1883); *S. australis* K.H. Barnard, 1916; *S. barnardi* Berge & Vader, 1997; *S. boxshalli* Berge *et al*., 2001; *S. calypsonis* Berge *et al*., 2001; *S. camoti* J.L. Barnard, 1967; *S. christianiensis* (Boeck, 1871); *S. gunnae* n.sp.; *S. ingstadi* n.sp.; *S. ledoyeri* Berge *et al*., 2001; *S. tori* n.sp.; *S. tucki* n.sp.; *S. wagini* (Gurjanova, 1936).

Species found in the area. *Stegocephaloides gunnae* n.sp.; *S. ingstadi* n.sp.; *S. tori* n.sp.; *S. tucki* n.sp.

Remarks. These are the first records of the genus *Stegocephaloides* in the area.

Stegocephaloides gunnae n.sp.

Figs. 11–13

Type material. HOLOTYPE: MV J40615, ♀ 5 mm: 38°16.40'S 149°27.60'E, 800 m, south of Point Hicks, Victoria, Australia, 23 Jun. 1986. Collector: M.F. Gomon and party. PARATYPES: MV J24059, 25 specimens: 38°16.40'S 149°27.60'E, 800 m, south of Point Hicks, Victoria, Australia, 23 Jun. 1986. Collector: M.F. Gomon and party.

Additional material. MV J24004, 1 immature, 37°07.30'S 150°20.20'E, 520 m, New South Wales, off Eden, 20 Jul. 86; MV J24056, 1 specimen, 38°24.14'S 149°13.07'E, 1220 m, Victoria, south of Point Hicks, 23 Jul. 1986; MV J40620, 24 specimens, 38°21.90'S 149°20.00'E, 1000 m, Victoria, south of Point Hicks, 23 Jul. 1986; MV J40621, 26 specimens, 38°19.60'S 149°24.30'E, 930 m, Victoria, south of Point Hicks, 23 Jul. 1986; MV J40626, 19 specimens, 42°2.20'S 148°38.70'E, 800 m, Tasmania, off Freycinet Peninsula, 27 Jul. 1986; MV J24062, 12 specimens, 42°0.20'S 148°37.70'E, 720 m, Tasmania, off Freycinet Peninsula, 27 Jul. 1986.

Distribution. Tasmania, Victoria and New South Wales, 500–1220 m.

Diagnosis (see also Table 3): Pleonites dorsally smooth. Antenna 1 flagellum with 5 articles. Antenna 2 peduncle article 4 as long as article 5. Epistome not produced laterally, epistomal plate present. Labrum as long as broad, left lobe reduced. Mandibular incisor toothed, lateral. Lacinia mobilis powerful, expanded laterally. Maxilla 1 outer plate with ST in a pseudocrown, palp uni-articulate. Maxilla 2 outer plate gaping and geniculate. Maxilliped palp dactylus simple and pointed. Pereopod 6 basis posteriorly expanded, expansion rudimentary. Uropod 3 outer ramus uni-articulate. Articulation between urosomites 2 and 3 absent. Telson longer than broad, pointed, cleft.

Description. Rostrum reduced, inconspicuous. Antenna 1 as long as antenna 2; accessory flagellum article 2 present. Antenna 2 peduncle articles 3–5 longer than flagellum; article 3 short, about as long as broad. Epistome curved (convex) and smooth; epistomal plate produced into a small

Table 3. Differences between the species of *Stegocephaloides* (for differences between *S. gunnae* and *S. tori*, see key above). A dash indicates either that morphological information is missing or that the character is inapplicable. Description of the characters—*character 1*: antenna 1 flagellum article 1, *a*, elongate, *b*, not elongate; *character 2*: antenna 2 peduncle article 4, *a*, about as long as article 5, *b*, shorter than article 5; *character 3*: epistomal plate, *a*, absent, *b*, present; *character 4*: maxilla 1 outer plate with an additional ST, *a*, absent, *b*, present; *character 5*: maxilla 1 palp articulation, *a*, absent, *b*, present; *character 6*: maxilliped palp dactylus, *a*, simple, *b*, cleft; *character 7*: pereopod 2 oostegite, *a*, well developed, *b*, reduced; *character 8*: pereopod 7 basis distally, *a*, rounded, *b*, pointed; *character 9*: uropod 3 outer ramus articulation, *a*, absent, *b*, present; *character 10*: uropod 3 outer ramus second article, *a*—long/ordinary, *b*—very short.

	characters									
species	1	2	3	4	5	6	7	8	9	10
Stegocephaloides attingens	a	a	a	a	a	a	b	b	a	–
Stegocephaloides auratus	a	b	a	a	a	a	a	b	a	–
Stegocephaloides australis	b	a	a	a	a	b	a	a	b	b
Stegocephaloides barnardi	b	a	a	a	a	a	a	a	a	–
Stegocephaloides boxshalli	b	a	a	b	a	a	a	a	b	b
Stegocephaloides calypsonis	b	a	a	a	a	a	a	a	b	a
Stegocephaloides camoti	b	a	a	a	a	a	a	a	b	b
Stegocephal. christianiensis	a	a	a	a	a	a	a	a	a	–
Stegocephaloides gunnae	b	a	b	a	a	a	a	a	a	–
Stegocephaloides ingstadi	b	a	a	a	a	a	a	a	b	b
Stegocephaloides ledoyeri	a	b	a	a	a	a	a	a	a	–
Stegocephaloides tori	b	a	b	a	a	a	a	a	a	–
Stegocephaloides tucki	a	a	a	a	a	b	a	a	a	–
Stegocephaloides wagini	a	a	a	a	b	a	a	a	a	–

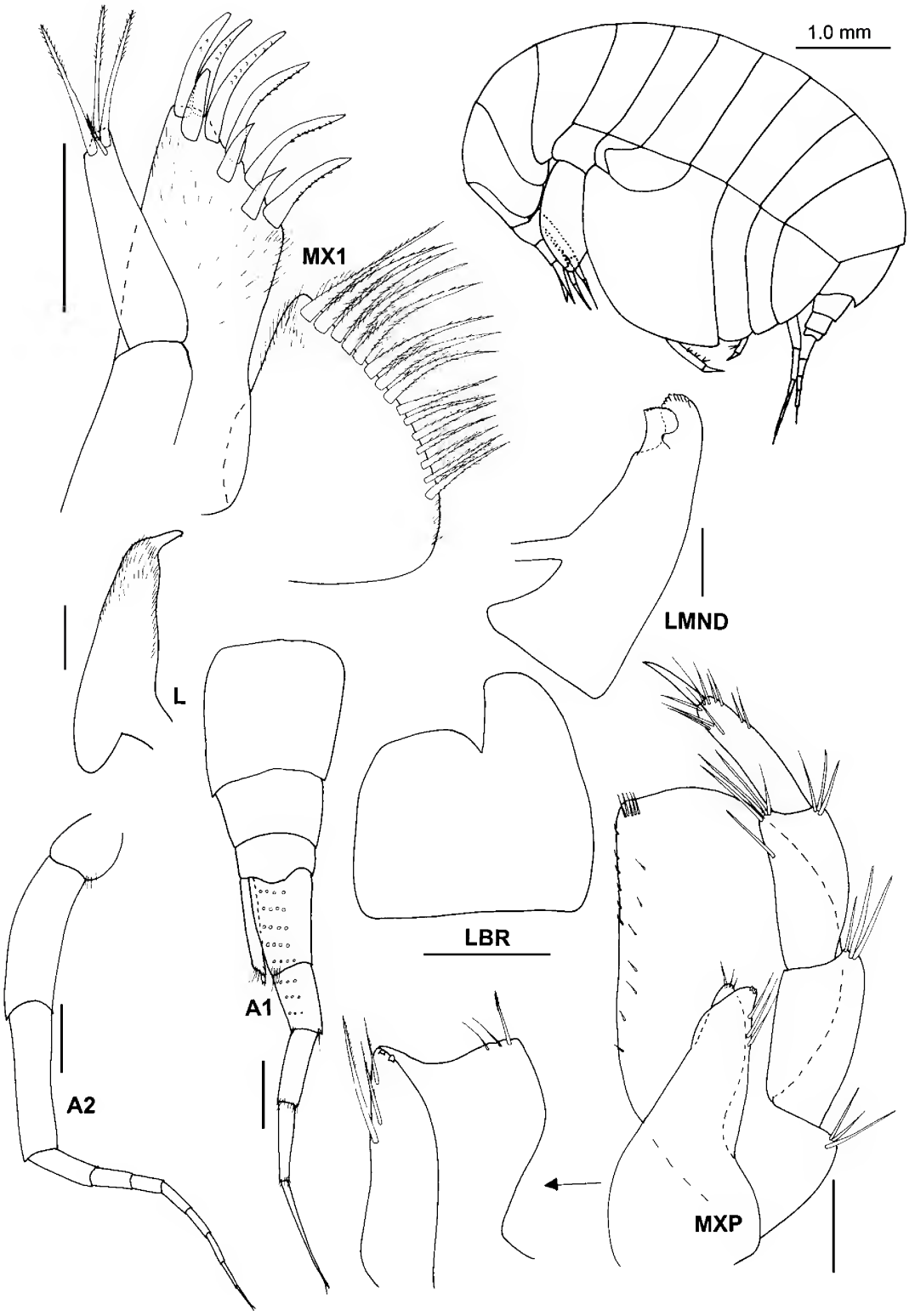

Fig. 11. *Stegocephaloides gunnae* n.sp. holotype, except *LMND* and *MXP IP*—J 24057 female A.

elongate medial ridge covering the entire epistome. Maxilla 1 palp not reaching above the apex of outer plate; outer plate distally subrectangular; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present, located distally, part of first row; ST B present, part of second row; ST C present; inner plate with pappocuspidate setae. Maxilla 2 outer plate setae with distal hooks, setae without distal cleft; inner plate setae row A covering about two thirds of the margin, clearly separated from row B; row A setae pappose; row B setae proximally pappose, distally with cusps present; row C present; row D present, expanded, row elongated towards and beyond row A, setae with many small cusps distally. Maxilliped palp 4-articulate; article 2 distal inner margin weakly produced; inner plate not exceeding base of palp article 2; 2 nodular setae; medial setae-row reduced and transverse, setae pectinate; distal setae-row present; inner setae-row reduced, setae not conspicuously large; outer

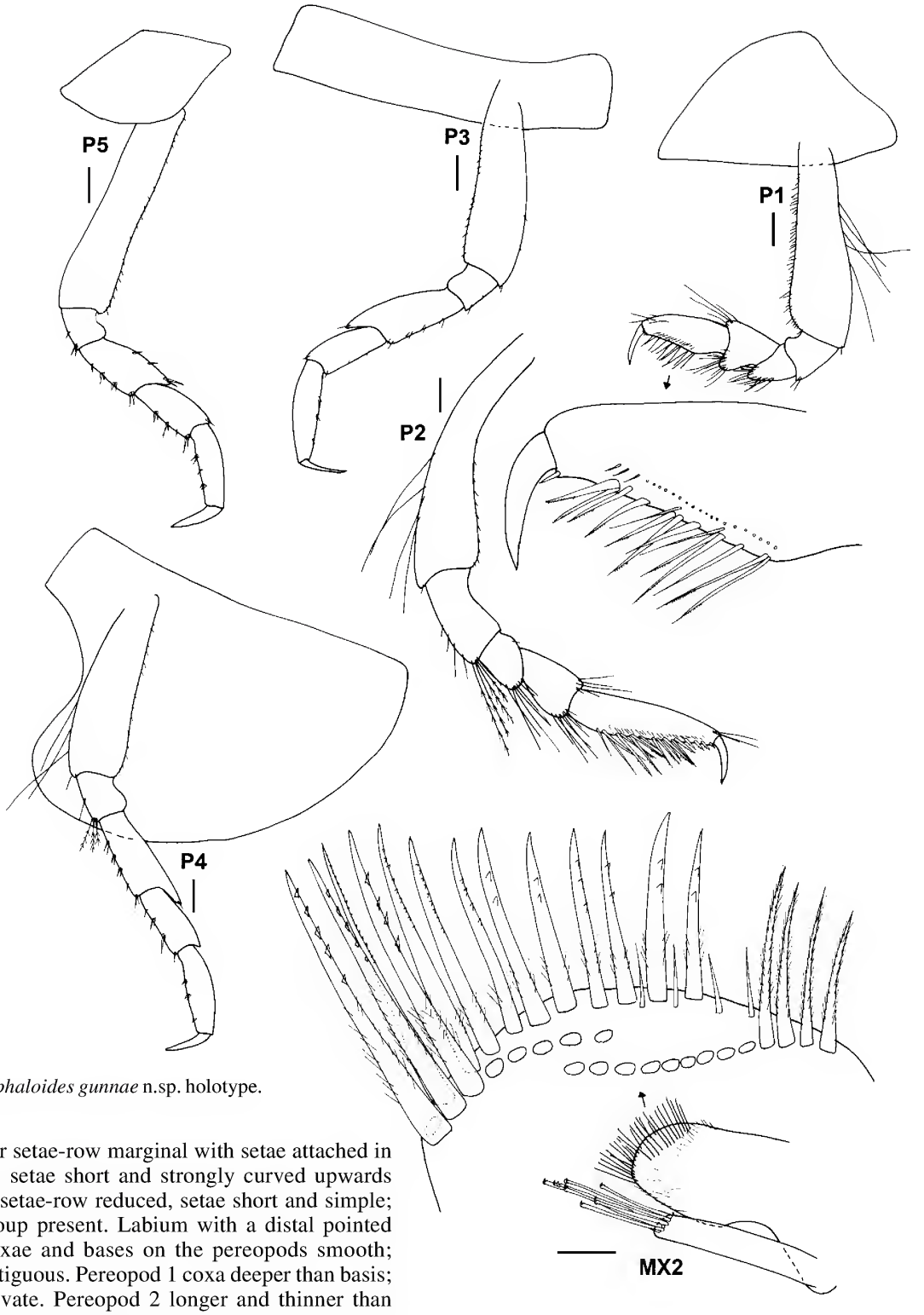

Fig. 12. *Stegocephaloides gunnae* n.sp. holotype.

plate with outer setae-row marginal with setae attached in a deep hollow, setae short and strongly curved upwards (hooks); inner setae-row reduced, setae short and simple; distal setae-group present. Labium with a distal pointed projection. Coxae and bases on the pereopods smooth; Coxae 1–3 contiguous. Pereopod 1 coxa deeper than basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length to breadth exceeding 1.5, distal posterior margin with plumose setae; propodus subrectangular but distally weakly narrowing, palm absent. Pereopod 4 basis posterior margin with long setae; ischium with plumose setae on distal posterior margin. Pereopod 6 basis submarginally with a row of long plumose setae. Pereopod 7 basis anterior margin straight, distally rounded; medial row of setae present, setae short and robust. Oostegites on pereopods 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus longer than inner. Uropod 2 peduncle as long as rami; outer ramus weakly longer than inner. Uropod 3 peduncle about half the length of rami; outer ramus as long as inner. Telson longer than peduncle uropod 3; submarginal setae on apex of each lobe absent.

Male. Pereopod 2 propodus larger in males than in females, urosome ordinary (similar to females).

Etymology. The present species is named after the first author's mother, Gunn Berge.

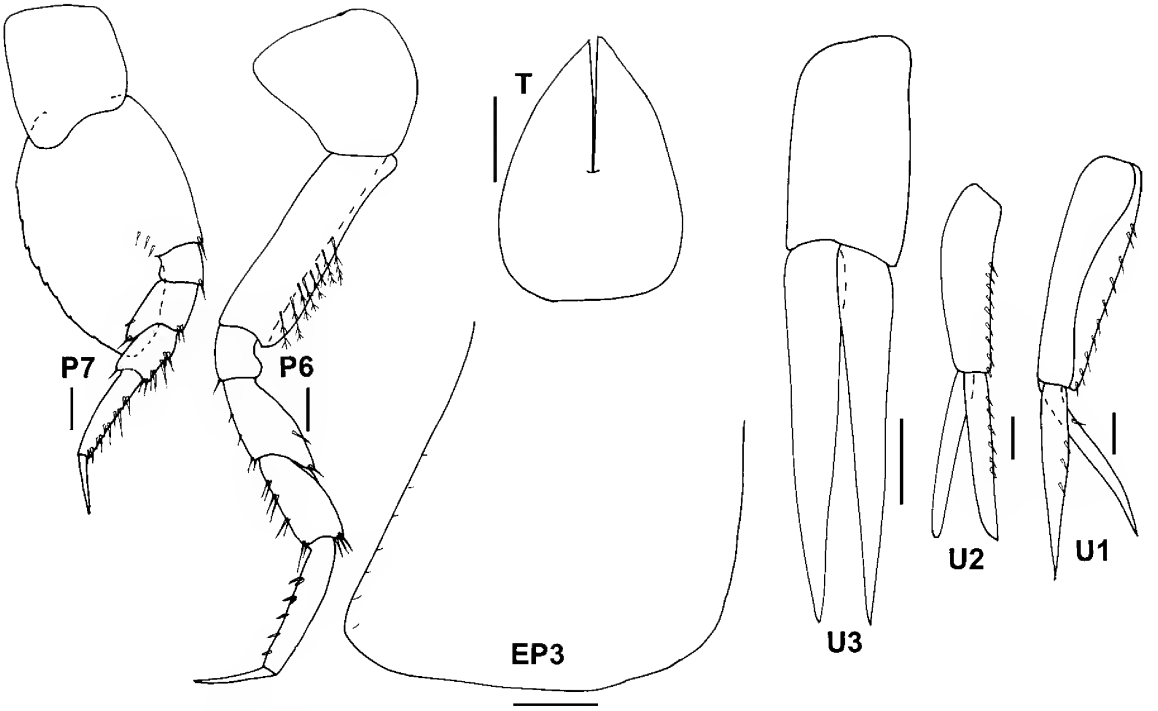

Fig. 13. *Stegocephaloides gunnae* n.sp. holotype except *U1, U2, U3* and *P2*—J 24057 female A.

Remarks. The morphology of the mouthparts, antennae, pereopod 6 and the uropods makes this a "typical" member of the genus, and closely related to *Stegocephaloides tori*. Both species are separated from its congeners mainly by the absence of several features (see Table 3), but also by the presence of an epistomal plate.

Stegocephaloides ingstadi n.sp.

Figs. 14, 15

Type material. HOLOTYPE: AM P50234, ♀ 5 mm, 16°37.81'S 146°23.08'E, 1000 m (QLD-931), east of Flynn Reef, Queensland, Australia, 06 Jun. 1993. Collector: J.K. Lowry & party on RV "Sunbird" (SEAS project, trap 2, transect 1).

Additional material. AM P60489, immature ♀ 4 mm, 30°10.94'S 153°32.27'E, 1000 m (NSW-863), NE of Coffs Harbour, New South Wales, Australia, 11 Aug. 1993. Collector: P. Berents & party on MV "Cheryl Lee". AM P49967, immature 2 mm, 30°13.75'S 153°28.56'E, 300 m (NSW-881), NE of Coffs Harbour, New South Wales, Australia, 12 Aug. 1993. Collector: P. Berents & party on MV "Cheryl Lee".

Distribution. known from the east coast of Australia (Queensland and New South Wales) at depths between 300 and 1000 m.

Diagnosis (see also Table 3): Pleonites dorsally smooth. Antenna 1 flagellum with 4 articles. Antenna 2 peduncle article 4 longer than article 5. Epistome not produced laterally, epistomal plate absent. Labrum longer than broad, left lobe reduced. Mandibular incisor toothed, lateral. Lacinia mobilis powerful, expanded laterally. Maxilla 1 outer plate with ST in a pseudocrown, palp uni-articulate. Maxilla 2 outer plate gaping and geniculate. Maxilliped palp dactylus simple and pointed. Pereopod 6 basis posteriorly expanded, expansion rudimentary. Uropod 3 outer ramus 2-articulate. Articulation between urosomites 2 and 3 absent. Telson longer than broad, pointed, cleft.

Description. Rostrum reduced, inconspicuous. Antenna 1 as long as antenna 2; accessory flagellum article 2 present. Antenna 2 peduncle articles 3–5 longer than flagellum; article 3 short, about as long as broad. Epistome curved (convex) and smooth. Maxilla 1 palp not reaching above the apex of outer plate; outer plate distally rectangular; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present, located distally, part of first row; ST B present, part of second row; ST C present; inner plate with pappocuspidate setae. Maxilla 2 outer plate setae with distal hooks, distal cleft absent; inner plate setae row A covering about two thirds of the margin, clearly separated from row B; row A setae pappose; row B setae proximally simple; distally with cusps present; row C present; row D present, row elongated towards and beyond row A, setae with many small cusps distally. Maxilliped palp 4-articulate; article 2 distally not produced; inner plate not exceeding base of palp article 2; 2 nodular setae; medial setae-row reduced and transverse, setae simple; distal setae-row present; inner setae-row not reduced, setae not conspicuously large; outer plate with outer setae-row marginal with setae attached in a deep hollow, setae short and strongly curved upwards (hooks); inner setae-row reduced with short and simple setae; distal setae-group present, setae short simple. Labium with a distal pointed projection. Coxae and bases on the pereopods covered with setae; setae very short. Coxae 1–3 contiguous. Pereopod 1 coxa about as deep as basis; propodus subrectangular but distally narrowing. Pereopod 2 longer and thinner than pereopod 1; ischium not elongate, distal posterior margin with plumose setae; propodus subrectangular but distally narrowing, palm absent. Pereopod 4 basis posterior margin with long setae; ischium with plumose setae on distal posterior margin. Pereopod 6 basis submarginally with a row of long plumose setae. Pereopod 7 basis anterior margin straight, distally rounded; medial row of setae present, setae short and robust. Oostegites on pereopods 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami;

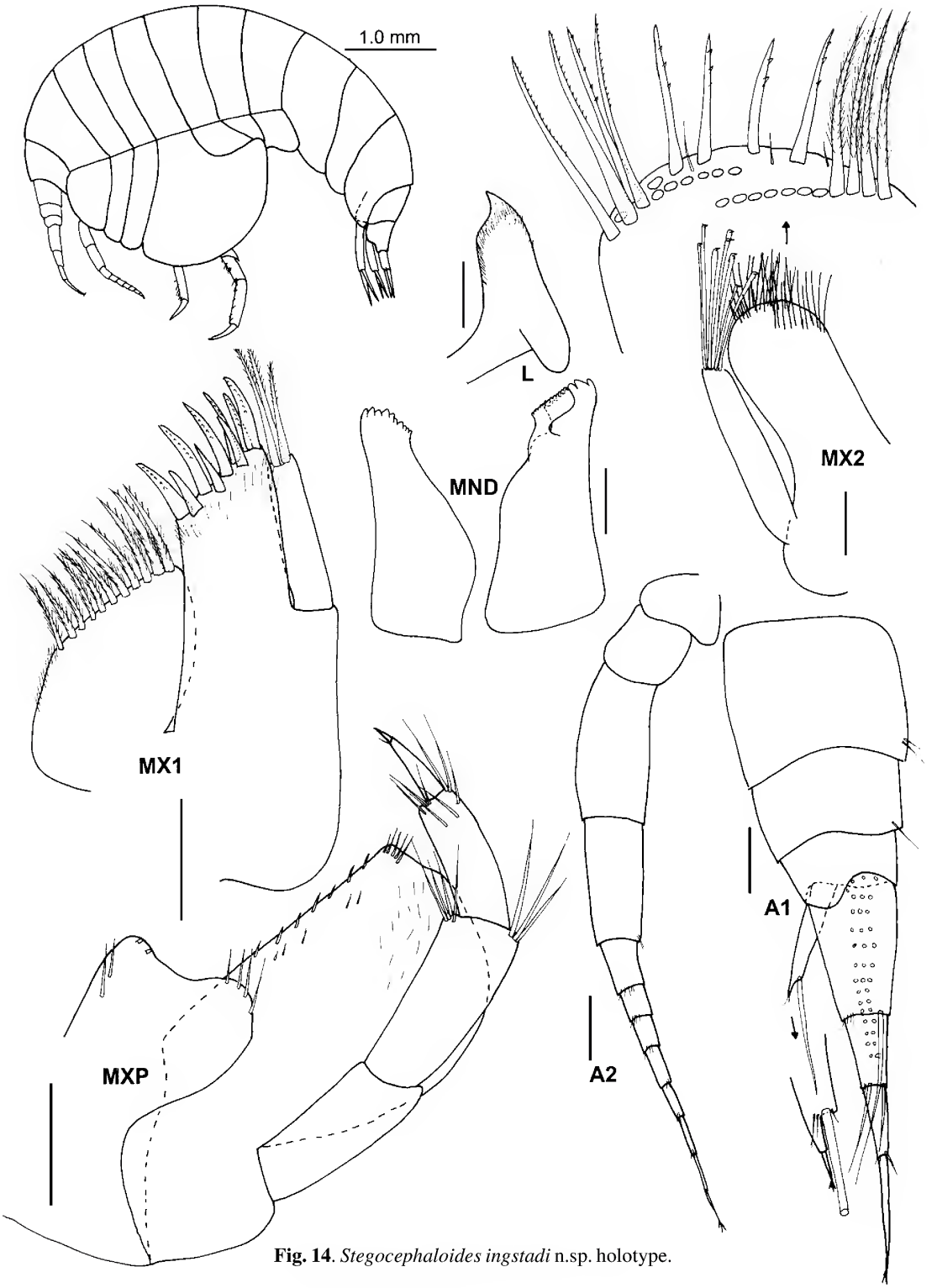

Fig. 14. *Stegocephaloides ingstadi* n.sp. holotype.

Table 4. Differences between *Stegocephaloides camoti* and *S. ingstadi* n.sp.

	species	
characters	***Stegocephaloides ingstadi***	***Stegocephaloides camoti***
antenna 1 flagellum	normal	flattened and inflated
labium, distal projection	pointed	crenulated
epimeral plate 3 posteroventrally	weakly produced, rounded	produced and acute/pointed
uropod 3 outer ramus	shorter than inner	longer than inner

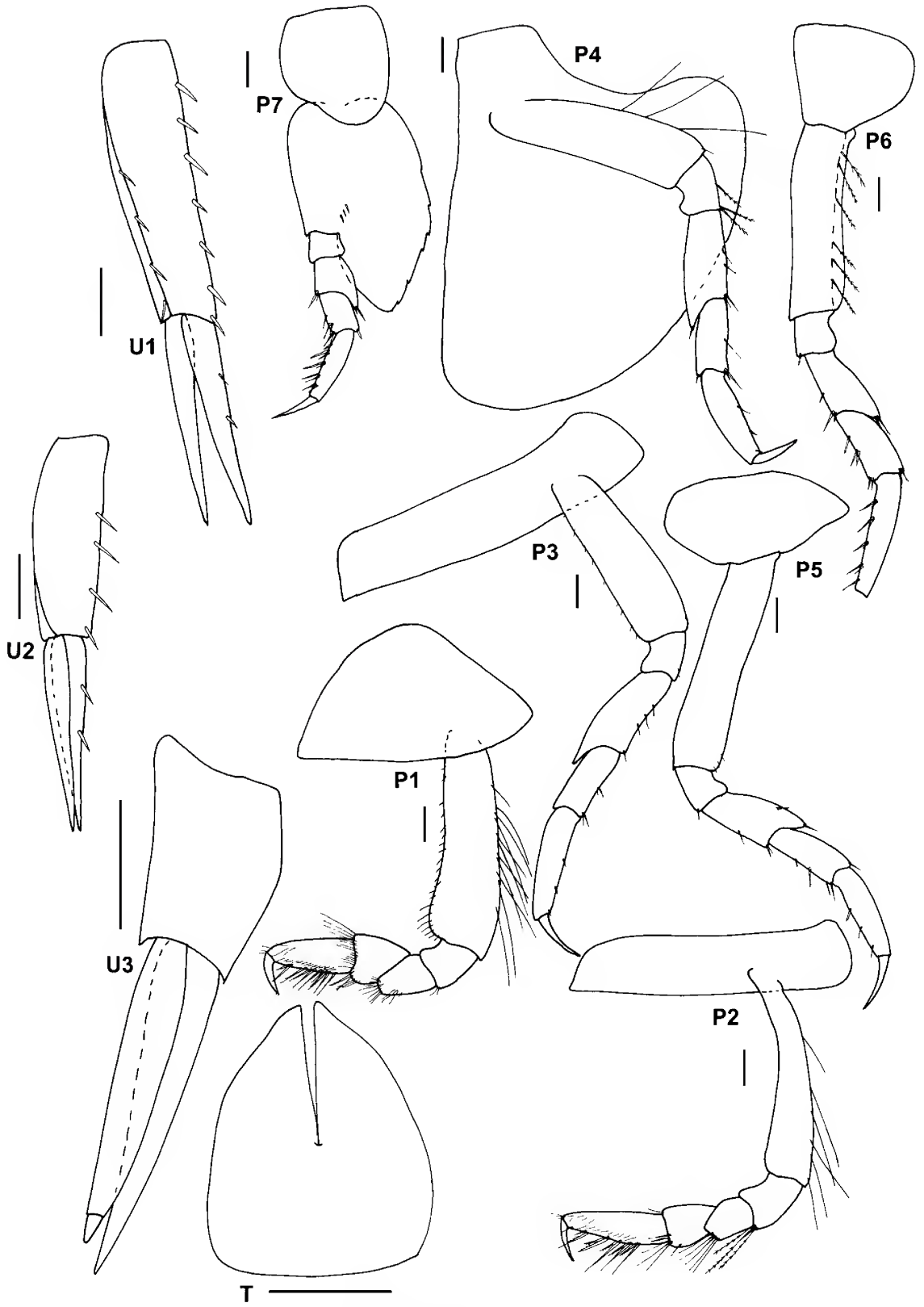

Fig. 15. *Stegocephaloides ingstadi* n.sp. holotype.

outer ramus weakly longer than inner. Uropod 2 peduncle as long as rami; outer ramus as long as inner. Uropod 3 peduncle shorter than half the length of rami; outer ramus shorter than inner. Telson longer than peduncle uropod 3; submarginal setae on apex of each lobe absent.

Male. Unknown.

Etymology. The present species is named after the Norwegian scientist, explorer and writer Helge Ingstad (1899–2001). Ingstad discovered remains of Viking settlements in North America built 500 years before the arrival of Columbus.

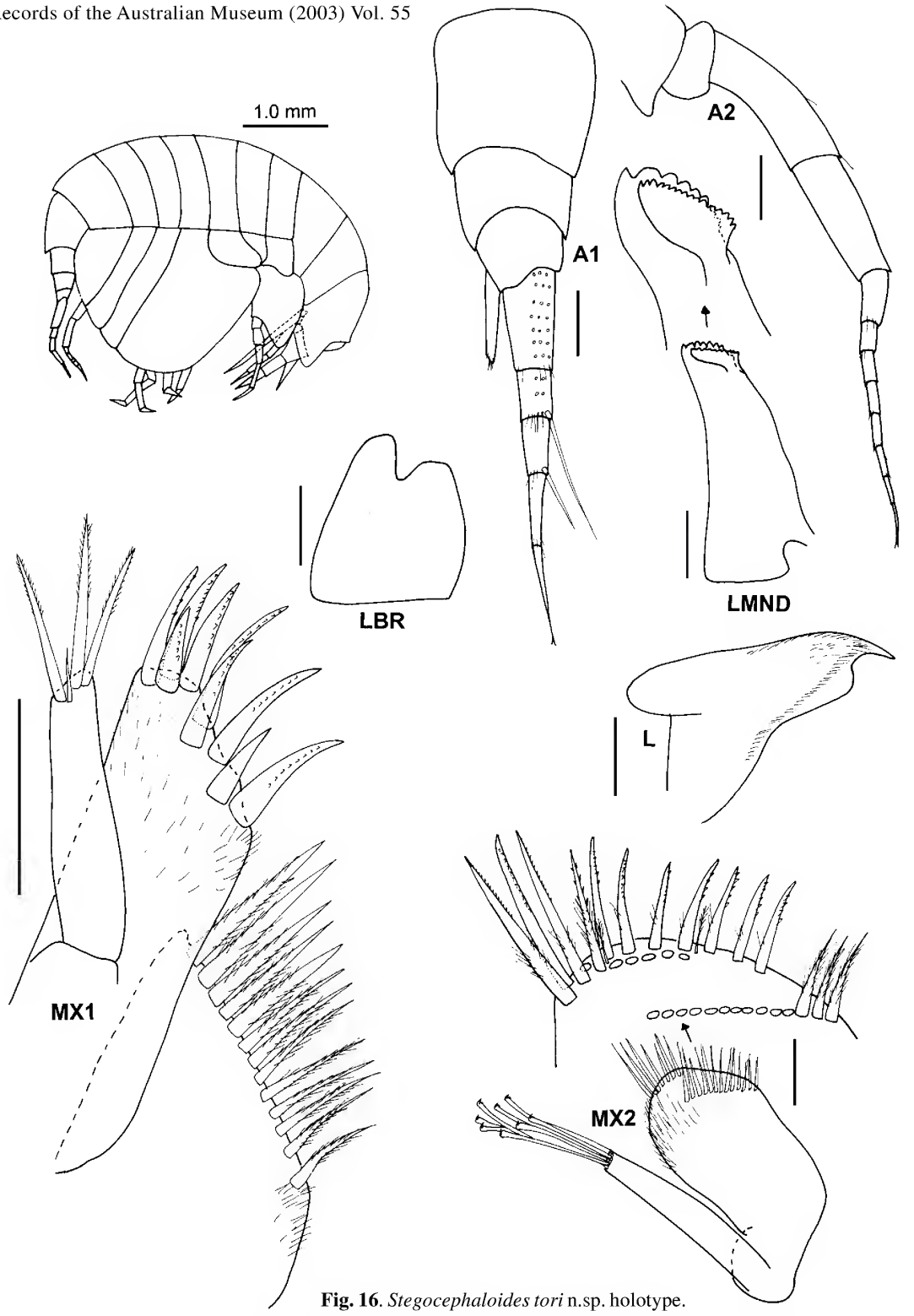

Fig. 16. *Stegocephaloides tori* n.sp. holotype.

Remarks. J.L. Barnard (1967) described *Stegocephaloides camoti* based upon a single specimen, which unfortunately has been inaccessible for examination. However, the material examined and described herein does show some distinctive and important differences from the holotype of *S. camoti* (see Table 4). First of all, J.L. Barnard (1967: 148) describes the first article of the flagellum of antenna 1 as "flattened and inflated (from lateral view)", and figures a distinctive crenulated distal projection on the labium. In *S. ingstadi*, the antenna 1 flagellum is round (the normal condition in the family), and the distal projection on the labium is pointed. Furthermore, *S. ingstadi* has the outer ramus on uropod 3 shorter than inner ramus, versus longer in *S. camoti*. Thus, although the two specimens appear to be closely related, a new species is erected for the Australian material.

Stegocephaloides tori n.sp.

Figs. 16–18

Type material. HOLOTYPE: MV J24054, ♀ 4 mm, 38°25.90'S 148°58.60'E, 1850 m, south of Point Hicks, Victoria, Australia, 22 Jul. 86. Collector: G.C.B. Poore and party.

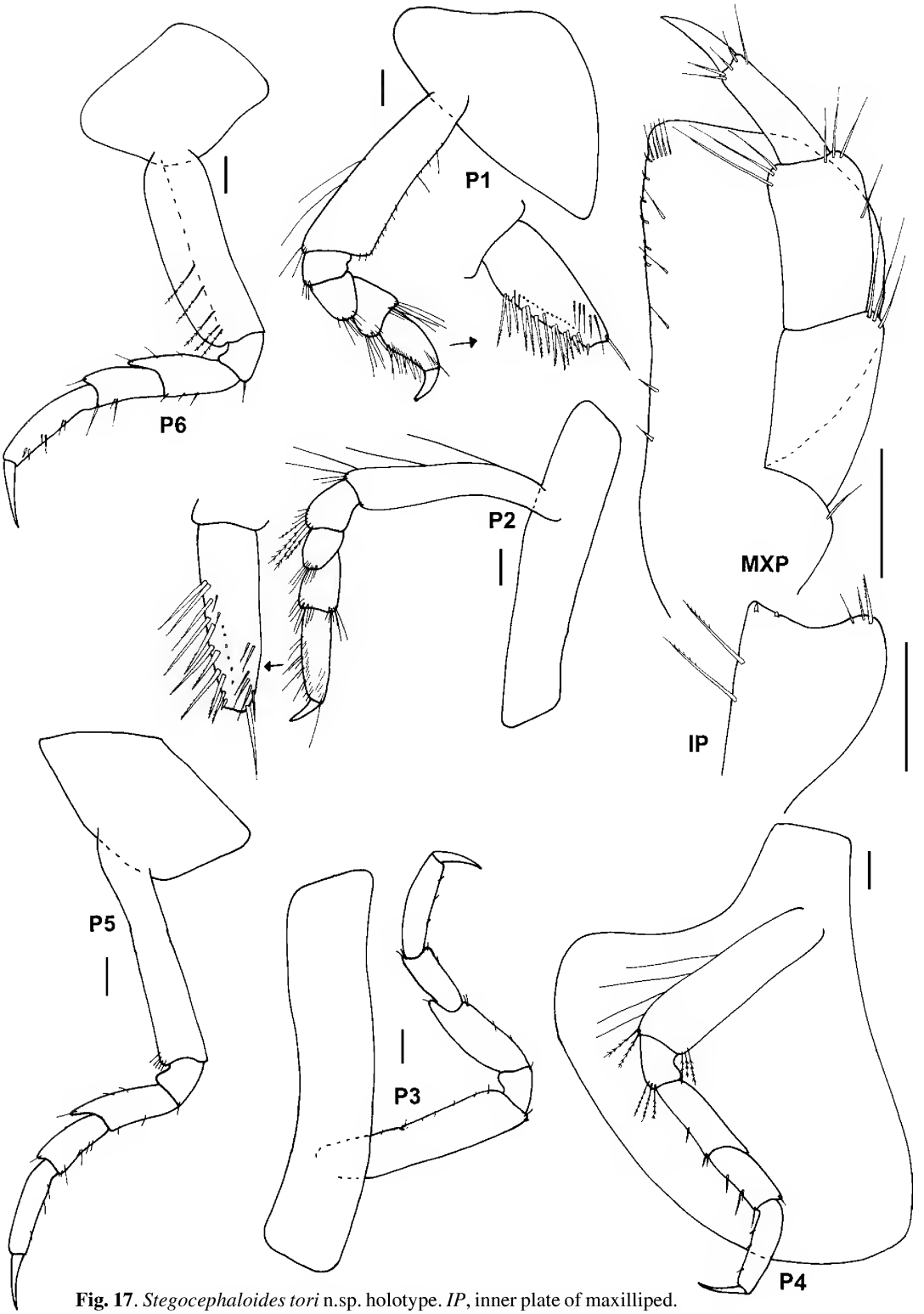

Fig. 17. *Stegocephaloides tori* n.sp. holotype. *IP*, inner plate of maxilliped.

Additional material. MV J24055, ♀ 4 mm, 38°25.00'S 149°0.00'E, 1500 m, south of Point Hicks, Victoria, Australia, 22 Jul. 1986; MV J45336, ♂ 3 mm, 38°52.6'S 148°25.2'E, 130 m, Eastern Bass Strait, Tasmania, Australia, 15 Nov. 1981.

Distribution. Bass Strait, 130–1850 m.

Diagnosis (see also Table 3). Pleonites dorsally smooth. Antenna 1 flagellum with 5 articles. Antenna 2 peduncle article 4 longer than article 5. Epistome not produced laterally, epistomal plate present. Labrum longer than broad, left lobe reduced. Mandibular incisor toothed, lateral. Lacinia mobilis powerful, expanded laterally. Maxilla 1 outer plate with ST in a pseudocrown, palp uni-articulate. Maxilla 2 outer plate gaping and geniculate. Maxilliped palp dactylus simple and pointed. Pereopod 6 basis expanded. Uropod 3 outer ramus uni-articulate. Articulation between urosomites 2 and 3 absent. Telson longer than broad, pointed, cleft.

Description. Rostrum reduced, inconspicuous. Antenna 1 longer than antenna 2; accessory flagellum article 2 absent. Antenna 2 peduncle articles 3–5 shorter than flagellum;

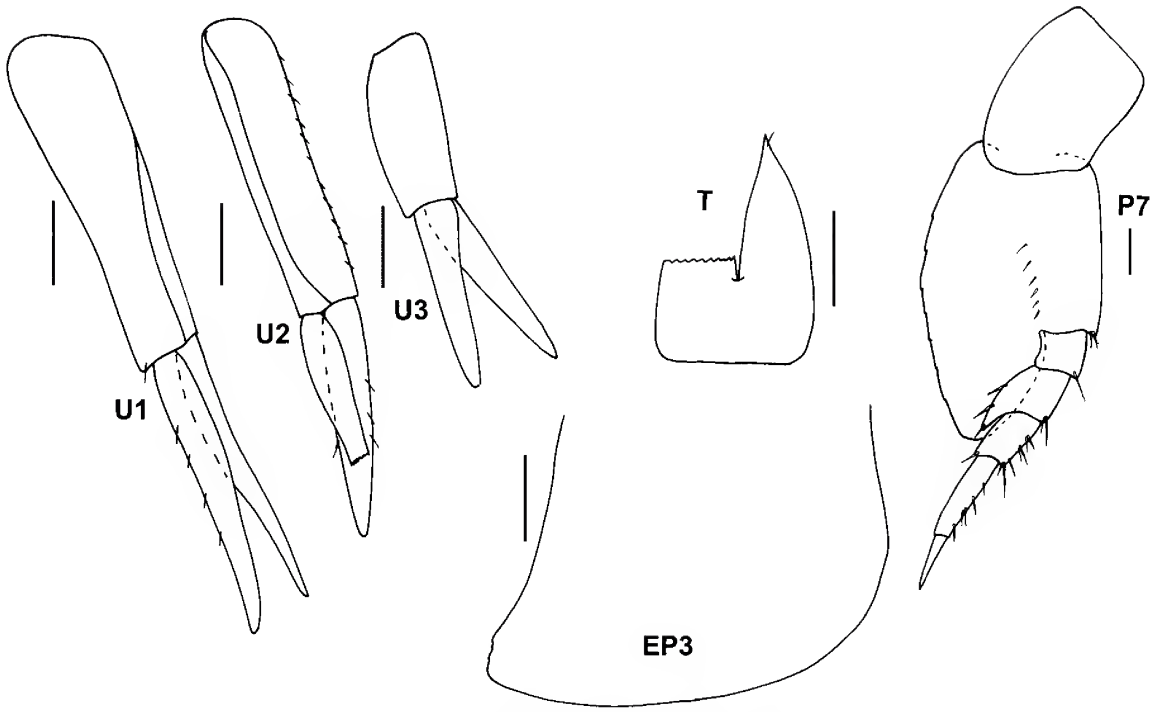

Fig. 18. *Stegocephaloides tori* n.sp. holotype.

article 3 short, about as long as broad. Epistome curved (convex) and smooth; epistomal plate produced into a small elongate medial ridge covering the entire epistome. Maxilla 1 palp not reaching above the apex of outer plate; outer plate distally subrectangular; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present, located distally, part of first row; ST B present, part of second row; ST C present; inner plate with pappose setae. Maxilla 2 outer plate setae with distal hooks, setae without distal cleft; inner plate setae row A covering about two thirds of the margin, clearly separated from row B; row A setae pappose; row B setae proximally pappose, distally with cusps present; row C present; row D present, expanded, elongated towards and beyond row A, setae with many small cusps distally. Maxilliped palp 4-articulate; article 2 distal inner margin weakly produced; inner plate not exceeding base of palp article 2; 2 nodular setae; medial setae-row reduced and transverse, with pectinate setae; distal setae-row present; inner setae-row not reduced, setae not conspicuously large; outer plate with outer setae-row marginal with setae attached in a deep hollow, setae short and strongly curved upwards (hooks); inner setae-row reduced, setae short simple; distal setae-group present, setae short simple. Labium with a distal pointed projection. Coxae and bases on the pereopods smooth. Coxae 1–3 contiguous. Pereopod 1 coxa deeper than basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length to breadth exceeding 1.5, distal posterior margin with plumose setae; propodus subrectangular, palm absent. Pereopod 4 basis posterior margin with long setae, distal anterior and posterior margins with plumose setae; ischium with plumose setae on distal posterior margin. Pereopod 6 basis about 1.5 times as broad as pereopod 5 basis, medially with a row of long plumose setae. Pereopod 7 basis anterior margin straight, distally rounded; medial row of setae present, setae short and robust. Oostegites on pereopods 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus weakly longer than inner. Uropod 2 peduncle longer than rami; outer ramus as long as inner. Uropod 3 peduncle longer than half the length of rami; outer ramus about as long as inner. Telson longer than peduncle uropod 3; submarginal setae on apex of each lobe present.

Male. Pereopod 2 propodus larger in males than in females; Urosome ordinary (similar to females).

Etymology. The present species is named after the first author's father, Tor Berge.

Remarks. See remarks under *Stegocephaloides gunnae*.

Stegocephaloides tucki n.sp.

Figs. 19–21

Type material. HOLOTYPE: AM P52713, ♂ 7 mm, 43°08.96'S 145°15.36'E, 1000 m (TAS-384), east of Fortescue Bay, Tasmania, Australia, 17 Apr. 1993. Collector: J.K. Lowry & party on MV "Tasmanian Enterprise" (SEAS project trap 2, transect 2). PARATYPES: AM P60409, 2♂♂, 6–7 mm, 43°08.96'S 145°15.36'E, 1000 m (TAS-384), east of Fortescue Bay, Tasmania, Australia, 17 Apr. 1993. Collector: J.K. Lowry & party on MV "Tasmanian Enterprise" (SEAS project trap 2, transect 2).

Additional material. MV J40623, 1♀, 38°16.40'S 149°27.60'E, 800 m, Victoria, south of Point Hicks, 23 Jun. 1986.

Distribution. Victoria and Tasmania, 800–1000 m.

Diagnosis (see also Table 3): Pleonites dorsally smooth. Antenna 1 flagellum with 9 articles. Antenna 2 peduncle article 4 shorter than article 5. Epistome not produced laterally, epistomal plate absent. Labrum longer than broad, left lobe reduced. Mandibular incisor toothed, lateral. Lacinia mobilis powerful, expanded laterally. Maxilla 1 outer plate with ST in a pseudocrown, palp uni-articulate. Maxilla 2 outer plate gaping and geniculate. Maxilliped

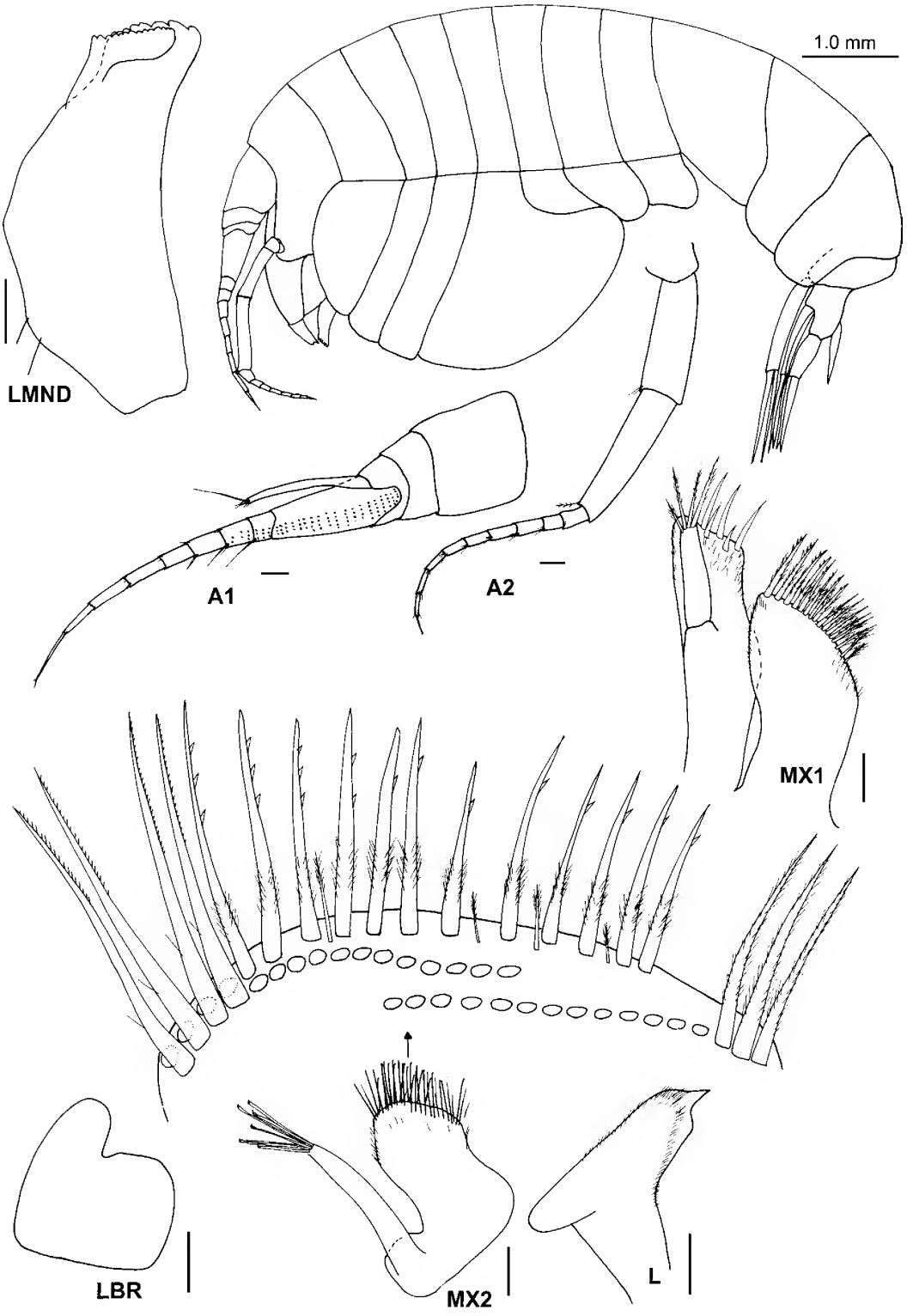

Fig. 19. *Stegocephaloides tucki* n.sp. holotype.

palp dactylus produced and bifid. Pereopod 6 basis posteriorly expanded, expansion rudimentary. Uropod 3 outer ramus uni-articulate. Articulation between urosomites 2 and 3 absent. Telson longer than broad, pointed, cleft.

Description. Rostrum reduced, inconspicuous. Antenna 1 longer than antenna 2; accessory flagellum article 2 present. Antenna 2 peduncle articles 3–5 longer than flagellum; article 3 short, about as long as broad. Epistome curved (convex) and smooth. Maxilla 1 palp not reaching above the apex of outer plate; outer plate distally subrectangular; ST first row with 6 setae (ST1–5, ST7); ST 6 absent; gap between ST 5 and ST 7 present; ST A present, located distally, part of first row; ST B present, part of second row; ST C present; inner plate with pappose setae. Maxilla 2 outer plate setae with distal hooks, setae without distal cleft; inner plate setae row A covering about two thirds of the margin, clearly separated from row B; row A setae pappose; row B setae proximally pappose, distally with

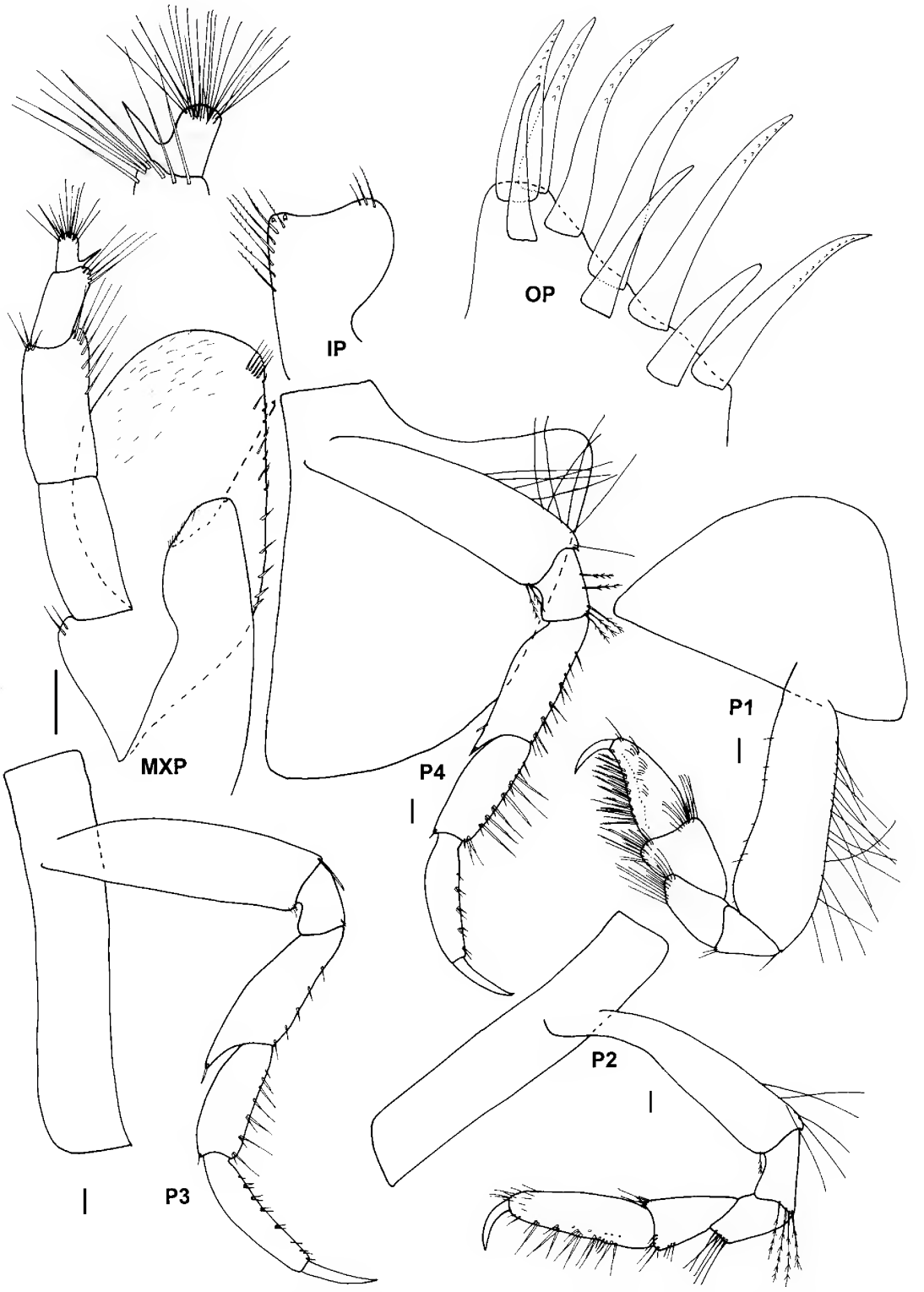

Fig. 20. *Stegocephaloides tucki* n.sp. holotype. *OP*, maxilla 1 outer plate; *IP*, inner plate of maxilliped.

cusps present; row C present; row D present, row elongated towards and beyond row A, with many small cusps distally. Maxilliped palp 4-articulate; article 2 distally produced; distal inner margin weakly produced; inner plate not exceeding base of palp article 2; 2 nodular setae; medial setae-row transverse, setae pectinate; distal setae-row present; inner setae-row not reduced; outer plate with outer setae-row marginal, setae short and strongly curved upwards (hooks); inner setae-row reduced, setae short and simple; distal setae-group present, setae short and simple. Labium with a distal pointed projection. Coxae and bases on the pereopods covered with setae; setae simple. Coxae 1–3 contiguous. Pereopod 1 coxa deeper than basis; propodus subovate. Pereopod 2 longer and thinner than pereopod 1; ischium elongate, ratio length to breadth exceeding 1.5, distal posterior margin with plumose setae; propodus subrectangular, palm absent. Pereopod 4 basis posterior margin with long setae; plumose setae on distal anterior margin; ischium with plumose setae on distal posterior margin. Pereopod 7 basis anterior margin straight, distally rounded;

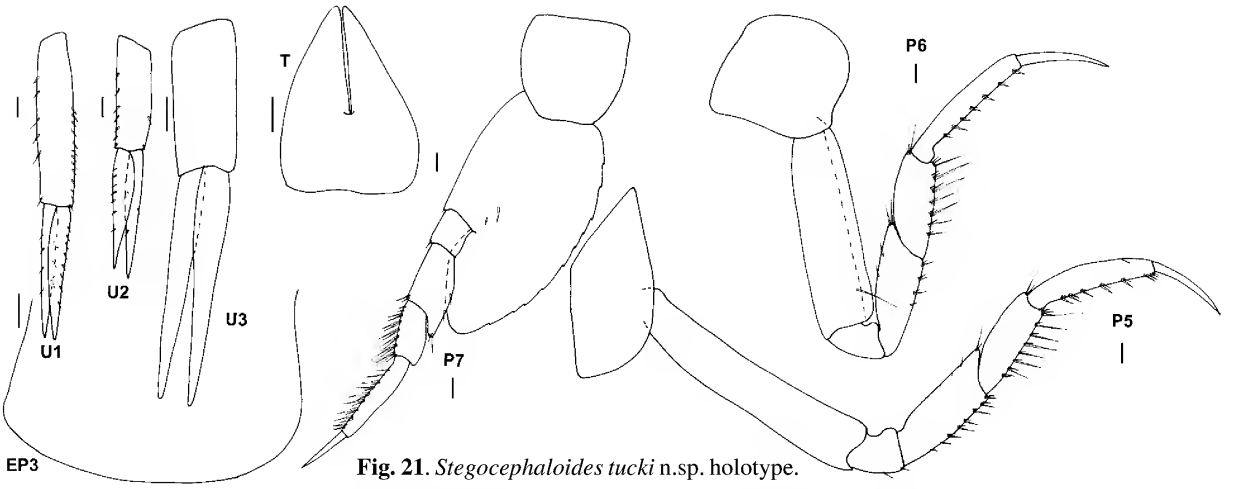

Fig. 21. *Stegocephaloides tucki* n.sp. holotype.

medial row of setae present, setae short and robust. Oostegites on pereopods 2–5, gills on pereopods 2–7. Uropods: Uropod 1 peduncle longer than rami; outer ramus as long as inner. Uropod 2 peduncle shorter than rami; outer ramus longer than inner. Uropod 3 peduncle longer than half the length of rami; outer ramus as long as inner. Telson longer than peduncle uropod 3; submarginal setae on apex of each lobe absent.

Male. Pereopod 2 propodus larger in males than in females; Urosome ordinary (similar to females).

Etymology. The present species is named after the very distinct morphology of its maxilliped palp: the dactylus is distally bifid, with one projection pointed and acute (most probably homologous to the dactylus found in other stegocephalids) and one blunt and heavily setose. The latter is distally slender but, seen from above, smooth with a dense collar of setae around. It is this arrangement of setae that the first author found similar to his childhood vision of the head of Friar Tuck, the good companion of the English hero, Robin Hood.

Remarks. This species and *Stegocephaloides australis* K.H. Barnard, 1916, are the only known species within the family that possess a cleft dactylus of the maxilliped palp (see Fig. 21). These two species can be separated on the absence of an articulation on outer ramus of uropod 3 and the long antennae in *S. tucki*.

Stegocephalopsis Schellenberg

Stegocephalopsis Schellenberg, 1925: 200.

Type species. *Cancer ampulla* Phipps, 1774.

Included species. *Stegocephalopsis ampulla* (Phipps, 1774); *S. latus* (Haswell, 1879); *S. mamillidacta* Moore, 1992; *S. pacifica* (Bulycheva, 1952).

Species found in the area. *Stegocephalopsis latus* (Haswell, 1879).

Remarks. *Stegocephalopsis latus* was one of the first stegocephalid species to be recorded from the area (Tasmania), but the species has never been sufficiently described. Only two specimens have ever been recorded, both from the type locality (Haswell, 1879, 1885). For a further discussion on this species, see Berge & Vader (2000).

Stegocephalopsis vegae Oldevig, 1959 was put into synonymy with the type of the genus, *S. ampulla* by Berge & Vader (2001a).

Stegosoladidus J.L. Barnard & Karaman

Stegosoladidus J.L. Barnard & Karaman, 1987: 869.
Stegosoladidus.–Berge, 2001a (revision).

Type species. *Andaniotes simplex* K.H. Barnard, 1930.

Included species. *Stegosoladidus antarcticus* Berge, 2001a; *S. complex* Berge, 2001a; *S. debroyeri* Berge, 2001a; *S. ingens* (Chevreux, 1906); *S. simplex* (K.H. Barnard, 1930).

Species found in the area. *Stegosoladidus complex* Berge, 2001a and *S. simplex* (K.H. Barnard, 1930).
Remarks. For a revision of the genus, and details about the species, see Berge, 2001a.

Tetradeion Stebbing

Tetradeion Stebbing, 1899: 207.
Tetradeion.–Berge & Vader, 2000: 170 (revision).

Type species. *Cyproidea crassa* Chilton, 1883.

Included species. *Tetradeion crassum* (Chilton, 1883) and *T. quatro* Berge & Vader, 2000.

Species found in the area. *Tetradeion crassum* (Chilton, 1883) and *T. quatro* Berge & Vader, 2000.

Remarks. For a revision of the genus, and details about the species, see Berge & Vader, 2000.

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